MODULATION OF BRAIN ACTIVITY BY THE INTEGRATION OF COLOR INTO DORSAL STREAM OBJECT FILES

SARA PARDISNIA

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Abstract

Two superimposed surfaces of dots are perceived as separate objects when rotating in two different directions. When one surface is cued, there is a larger suppression of the attentional ERP components of the unattended surface than the attended surface when two objects are perceived versus when one object is perceived. We hypothesized that the strength of object-based attention was dependent on the differentiation of the two object representations. We tested this hypothesis by determining if two oppositely rotating superimposed surfaces of differing colors would produce a greater cueing effect than if the two surfaces were the same color. This additional color feature would allow for object files with stronger neural representation, leading to a greater suppression of the uncued surface in the task. It was found that there was a greater cueing effect in the bicolored condition compared to the unicolored condition both behaviorally and in event related potentials.

Dedication

I would like to dedicate this thesis to my parents, Farhad and Farnoosh Pardisnia. You have been the ultimate example of hard work and through the years you have shown me how to persevere in the face of any challenge. Throughout all of the times I came home tired and stressed and feeling defeated, you were there to listen, to pick up the pieces, and put me back together. You believed in me wholeheartedly and stood behind me in my weakest moments to ensure I only ever moved forward. I am incredibly lucky to have such a great support system and I owe all of my accomplishments to the both of you. Thank you mom and dad.

Lots of love,

Sara

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EEG – Electroencephalogram

ERP – Event Related Potential

IT – Inferior Temporal Cortex

LGN – Lateral Geniculate Nucleus

LPC – Late Positive Component

M – Magnocellular

MO-ERP – Motion Onset - Event Related Potential

MST – Medial Superior Temporal

MT – Medial Temporal

N1 – First Negative Component

N2 – Second Negative Component

N2pc – Second Negative Subcomponent Posterior-Contralateral

P – Parvocellular

P1 – First Positive Component

P2 – Second Positive Component

P3 – Third Positive Component

RDK – Random Dot Kinetograms

SOA – Stimulus Onset Asynchrony

TE – Anterior Inferior Temporal Cortex

TEO – Posterior Inferior Temporal Cortex

V1 – Primary Visual Cortex

V2 – Visual Area Two

V3 – Visual Area Three

V4 – Visual Area Four

Chapter 1: General Introduction

Feature Integration

As we go through our daily lives, our brain is taking in thousands of pieces of information and processing them in order so that we perceive an accurate interpretation of the world around us. It is meticulously making calculations and one of these very important calculations is the way in which the brain puts together features into entire objects. "The world with which we interact consists of coherent and unitary objects that comprise many features, rather than an unstructured collection of localized image fragments" (Wertheimer, 1923).

The Gestalt principles of perceptual organization were one of the first theories that helped to define objects. These principles consisted of: grouping by similarity, proximity, connectedness, good continuation, common fate, and grouping by common region (Wertheimer, 1923, 1950), and provided a framework by which objects were constructed from local elements or features. Physiological studies have shown that a visual display is processed in the brain by neurons that are specialized for features such as orientation, color, spatial frequency, and movement and these features are mapped in specific regions of the brain (Zeki, 1976). Thus, certain areas of the brain process specific features of a visual display; however it is unknown how these features are integrated so that we perceive a unified precept. What mechanism is needed to bring together the incoming data that is relevant to one object, bind it together, and separate it from other objects? This is known as the binding problem (Treisman, 1996).

Feature Integration Theory

One potential mechanism, feature integration theory, posits that features of an object are processed first and are then bound by spatial location to form an *object file* and compared to stored representations to identify the object (Treisman et al., 1977). Before explaining this theory

further, it is important to define the different forms of attention. Attention is the preferential processing of a section of a visual scene. There are two types of attention; bottom up attention and top down attention. Bottom up attention (exogenous attention) occurs when attention is drawn to an object due to its saliency in comparison to the objects in the background. For example, when looking at a scene, attention is drawn to the white spot in a black background (Corbetta et al., 1993). Top down attention (endogenous attention) occurs when attention is drawn to an object due to previous knowledge or experience or a goal that is in place. For example, when looking at a scene, attention is drawn to the red berries in a green plant when the observer is looking for red berries to pick (Treisman & Gelade, 1980). Top down attention is dependent on tasks that require attending to a location in space, a feature, or an object. Thus, the subsets of top down attention are spatial attention, feature-based attention, and object-based attention.

After a series of experiments were conducted, Treisman and Gelade (1980) concluded that in feature integration theory, we become aware of unified objects through focal attention and top-down processing. In this theory, features are considered to be perceived before objects. Treisman had stated "features are registered early, automatically, and in parallel across the visual field, while objects are identified separately and only at a later stage, which requires focused attention" (Treisman & Gelade, 1980). Treisman defined features as being values in dimensions such as color, orientation, spatial frequency, brightness, and direction of movement. The initial path to object recognition depends on features present in the same central fixation of attention or spatio-temporal spotlight being integrated to be part of the same object. When the integration is completed, the object is stored as an object file and continues to be perceived in that form. The second path to object identification is through top-down processing where in a familiar context

possible objects can be predicted and their presence can be determined by corresponding their disjunctive features to those in the display (without determining their spatial integration) (Treisman & Gelade, 1980). As a result, top down (endogenous attention) processing of unattended features can use past experience as well as context in order to determine an object. Treisman explained how with a loss of memory or interference, these features can split from one another and reform in an incorrect manner to form what is called "illusory conjunctions" (Treisman et al., 1977). An example of an illusory conjunction is having a blue square and a purple triangle in front of the participant and the participant perceiving a blue triangle.

The object file is an intermediate representation that contains the bound features of the object and leads to recognition of the object, which is stored in long-term memory. If the object file matches a template that already exists in the brain, the person receives the semantic information. Otherwise, the object file is used to store new semantic information (Kahneman et al., 1992). Thus, processing a visual object forms an "object file" and this file contains information about the features of the object and some knowledge about the object, which is stored in long-term memory. The information about the object can then be maintained even when sensory input is not present. When one sees a familiar object that has most of the original features, the object file is retrieved and updated. However, a new object requires a new file to be made. Remington et al. (1992) went on to show that our brain can keep track of 4 items at a time through keeping 4 object files open simultaneously.

Marr (1982) described a similar concept in his visual theory. The brain initially forms a primal sketch of the object where intensity changes and their geometric organization are detected in the 2D sketch of the object that allows for representation of virtual lines and boundaries. Afterward, the brain forms a 2.5D sketch of the object that includes the representation of the

surfaces and their orientation and basic information about depth. Finally, a 3D model of the object is formed in the brain that includes the representation of shapes and their spatial recognition. This 3D model provides object recognition. The intermediate object file is thought to be an analog of Marr's 2.5D sketch. Nakayama et al. (1995) have suggested that intermediate object representations are the substrate for object-based attention. They suggest that object-based attention selects surfaces, which are intermediate object representations produced by combining the initial features of the object but before more complex visual processing such as a 3D representation and object recognition.

Visual Processing Streams

The binding problem is further complicated by the fact that visual processing is split into two parallel, but interconnected, streams. When the eyes take in information, the image on the retina is transferred through the optic nerves, the optic chiasm, and through the optic tracts. The optic tracts then project this information onto the lateral geniculate nucleus (LGN). The LGN divides into the parvocellular (P) and magnocellular (M) pathways. The magnocellular cells are sensitive to low luminance, low spatial frequencies and high temporal frequencies. The parvocellular cells are selective for color, high contrasts, high spatial frequencies, and low temporal frequencies. Both M and P cells project onto layer 4C of the primary visual cortex (V1) consisting of color blobs and interblobs. In this area, the interblobs are sensitive to the motion of moving edges, bars, and gratings and their orientations and direction (Hubel & Wiesel, 1968; Hubel et al., 1978; Adelson & Bergen, 1985; Orban et al., 1986; Movshon & Newsome, 1996). The blobs are sensitive to color (Solomon et al., 2004; Solomon & Lennie, 2005). Once in V1, the P and M pathways are the ventral and dorsal streams respectively. Within each stream, hierarchical processing builds on information from the previous stage and increases the

complexity of the visual representation.

The dorsal stream travels from V1 to V2 and then to the medial temporal (MT) and medial superior temporal (MST) regions of the brain and then finally ends in the posterior parietal cortex (for review see Burr & Thompson, 2011). Area MT and MST are only present in monkeys; in humans motion processing occurs in a combined area termed MT+ that performs the functions of both area MT and MST from the monkey studies. The dorsal stream is responsible for processing the speed, spatial frequency, direction and depth. In area V2 there are thick, thin, and pale stripes, and each set of stripes receives distinct input information (Hubel & Livingstone, 1987; Levitt et al., 1994). Following V2, information is transferred to area MT, in fact V2 is the second largest input into MT (DeYoe & Van Essen, 1985; Shipp & Zeki, 1985; Born & Bradley, 2005). Area MT is sensitive to speed (Maunsell & Van Essen, 1983; Lagae et al., 1993; Perrone & Thiele, 2001; Priebe et al., 2003; Brooks et al., 2011), direction (Maunsell & Van Essen, 1983; Albright, 1984; Lagae et al., 1993), spatial frequency, temporal frequency (Priebe et al., 2003; Brooks et al., 2011), and local/global motion (Pack & Born, 2001; gratings: Adelson & Movshon, 1982; Rodman & Albright, 1989; random dot kinetograms (RDKs): Britten et al., 1992; Snowden et al., 1992). Once two dimensional motion processing is completed in area MT, information is forwarded to area MST where three dimensional motion processing occurs. MST processes expansions, contractions, rotations (Saito et al., 1986), translations, spirals (Graziano et al., 1994; Mineault et al., 2012) and optic flow (Duffy & Wurtz, 1991a,b). Beyond MST, the information is transferred to the parietal regions of the brain responsible for processing heading, optic flow, self-motion, and multimodal integration (Phinney & Siegel, 2000; Raffi & Siegel, 2007; Raffi et al., 2010; Chen et al., 2013; Raffi et al., 2014;). Models of motion processing along the dorsal stream have focused on algorithmic motion computations (Burr & Thompson,

2011; Nishida, 2011) not object representations.

The ventral stream travels from V1 through V4 and to the inferior temporal cortex (IT). Area IT is present in both humans and monkeys; however, the human and monkey brain differ slightly in the areas between V4 and IT. The ventral stream is responsible for features such as form and color of objects (van Essen & Gallant, 1994). From area V1, information is projected to area V2 to the thin stripes and interstripes. Color processing occurs here along with form processing such as edges, illusory edges, and border ownership (von der Heydt et al., 1984; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; Zhou et al., 2000). Following V2, information is forwarded to area V4 which is sensitive to angles, curvature, perceived color, kinetic contours, and motion (Schein & Desimone, 1990; Pasupathy & Connor, 1999; Orban, 2008; Pasupathy & Connor, 2001; Mysore et al., 2006; Ferrera et al., 1992, 1994; Li et al., 2013). Once the information reaches area IT, simple shapes are processed in the posterior IT or the TEO (Tanaka et al., 1991; Kobatake & Tanaka, 1994). Area TEO is only present in monkeys. More complex shapes are processed in the anterior IT or TE (Gross et al., 1972; Desimone et al., 1984; Tanaka et al., 1991). Area TE is only present in monkeys. This is where objects are represented and object recognition occurs (Cowey & Weiskrantz, 1967; Gross et al., 1971, 1972; Dean, 1976). Furthermore, this region processes body parts as well as object invariance (see Gross, 2008 for a review; Sato et al., 1980; Schwartz et al., 1983; Rolls & Baylis, 1986; Ito et al., 1995; Logothetis & Pauls, 1995; Sáry et al., 1993). Understanding the processing along the ventral stream has led to the development of object representation models (e.g. Marr & Nishihara, 1978. See Peissig & Tarr, 2007 for a review).

Ventral Stream Object Representations

Object recognition is a process that we are coming to understand more and more. Marr and Nishiara (1978) proposed the 3-D model representation suggesting that objects consisted of parts that are spatially close to one another. These parts are represented in the brain as generalized cones or cylinders and the identification of objects takes place at a higher stage of processing. Marr and Nishiara wanted a representation of an object that fit computational criteria. This representation needed to be accessible, unique, generic, stable and sensitive. One challenge faced was that as a three-dimensional object moves, the two-dimensional view of the object changes (viewpoint invariance). To solve this problem, the theory posited that the cones are object-centered representations, independent of the orientation of the object.

The recognition by components model (Biederman 1985) introduced the idea of properties to indicate shape called Geons. These properties define if the object consists of a straight or curved edge, if the object is symmetrical, if the object expands or contracts. This model also defined spatial properties such as beside or below as well as developed viewpoint-invariant properties. This model, however, did not represent any stages beyond the basic level of object recognition.

While the earliest theories focused on viewpoint invariant representations, later theories were developed that allowed for viewpoint-dependent object representations (e.g. Poggio & Edelman, 1990; Lawson et al., 1994). The viewpoint-dependent models provided evidence for objects being recognized through matching images or image descriptions to view-specific stored representations (Lawson et al., 1994). Gross and colleagues found that while V1 and V2 have been associated with simple stimuli, higher level regions such as IT are not responsive to simple stimuli but rather to complex stimuli, thus supporting object representations at the highest levels (Gross et al., 1969, Gross et al., 1972). Shapes in conjunction with color or texture (Gross et al.,

1972; Desimone et al., 1984; Tanaka et al., 1991), as well as hands and faces can all be processed and recognized in area IT (see Gross, 2008 for a review). The neurons in area IT are viewpoint and size invariant, providing evidence that object-files are present in the ventral stream and are representing objects regardless of their size and position (Sato et al., 1980; Schwartz et al., 1983; Rolls & Baylis, 1986; Ito et al., 1995; Logothetis & Pauls, 1995). As well, it has been shown in neurophysiology research that different patterns of firing occur for different objects in area IT. Thus, there is strong evidence for object-files in the ventral stream (Mitroff et al., 2005, 2007, 2009; Noles et al., 2005).

Dorsal Stream Object Representations

There are multiple studies showing cross-talk between the dorsal and ventral streams (Schiller, 1993; Sereno & Maunsell, 1998; Tsutsui et al., 2001; Sereno et al., 2002; Peuskens et al., 2004; Durand et al., 2007; Lehky & Sereno, 2007; Wannig et al., 2007; Konen & Kastner, 2008; Tchernikov & Fallah, 2010; Perry & Fallah, 2012). Recent studies support the existence of object files in the dorsal stream (Perry et al., 2014; for review see Perry & Fallah, 2014), that also include ventral stream features (e.g. color: Tchernikov & Fallah, 2010; Perry & Fallah, 2012; 2014).

Studies have shown that people with visual agnosia (ventral stream damage) are not able to recognize objects, yet they are able to place their hand in the correct orientation and grip in order to grasp an object (Goodale et al., 1991, 1994; Milner et al., 2012). Similarly, reaching and grasping actions show knowledge of object orientation, shape, and size without conscious awareness (Taira et al., 1990; Gallese et al., 1994; Murata et al., 2000; Fattori et al., 2005). This provides support for cross-talk between the ventral and dorsal streams and the possibility of object files in the dorsal stream. Similar to how the ventral stream integrates features from the

dorsal stream to eventually lead to object recognition in structure-from-motion stimuli (Johansson, 1973, 1976; Siegel & Andersen, 1988), the dorsal stream integrates features into the object files for decision-making processes about motion perception.

Color and Motion

Two superimposed random dot kinetograms (RDK) moving in different directions are perceived to be repulsed from each other, called direction repulsion (Marshak & Sekuler, 1979; Mather & Moulden, 1980; Hiris & Blake, 1996; Braddick et al., 2002; Curran & Benton, 2003; Perry & Fallah, 2012). This illusion occurs due to the different motion directions mutually inhibiting one another and thus causing the two stimuli to be further discriminated from one another (Marshak & Sekuler, 1979; Mather & Moulden, 1980; Wilson & Kim, 1994; Kim & Wilson, 1996; Perry et al., 2014) putatively in area MT (Wilson & Kim, 1994; Kim & Wilson, 1996; Benton & Curran, 2003). In fact, research has shown that the two directions may be perceived as being up to 20 degrees further apart from each other than they actually are (Marshak & Sekular, 1979) and this phenomenon occurs on superimposed dot fields that are moving up to 110 degrees from each other (Mather & Moulden, 1980). Furthermore, with increased speed and density, less direction repulsion occurs, implying that direction repulsion occurs for global motion and not local motion (Braddick et al., 2002). It has also been shown when the two superimposed RDKs differ in speed from one another, the extra information allows better discrimination of the two surfaces from each other, decreasing mutual inhibition, and thus decreasing direction repulsion.

Perry and Fallah (2012) added support to this hypothesis by showing that when the surfaces were of differing colors, the repulsion was not affected, but instead the addition of color differences increased processing speed of direction judgments. The faster responses occurred due

to faster decision making occurring by reducing the noise in the noisy walk to threshold (Shadlen & Newsome, 1996, 2001). Thus when the two surfaces differed in color, color could be used to select one surface over the other and therefore reducing the motion information and essentially filtering out the noise from the second surface. This requires that decision-making works on object files such that object-based selection could occur (Duncan, 1984). This study supported prior studies that had showed that attention could indeed be focused on one of two superimposed surfaces, wherein participants were better at determining the direction of a brief translation of one of two counter-rotating superimposed surfaces when it was cued versus uncued (Valdes-Sosa et al., 1998, 2000; Reynolds et al., 2003).

Further evidence for dorsal stream object files emerged when it was shown that judging the direction of a brief translation of one of two superimposed surfaces was improved when that surface was endogenously cued by its color. As well, Mitchell et al in 2003 showed it was the object, not the color, that mattered, and thus providing further evidence of surface based attention and thus selection due to the presence of an object file.

Following their 2012 color integration study, Perry et al. (2014) set out to find if speed segmentation cues could reduce processing time as well as affect direction perception. MT neurons process local (component) and global (pattern) motion (Britten, Shadlen, Newsome, & Movshon, 1992; Recanzone, Wurtz, & Schwarz, 1997) and can decipher between global motion direction and the direction of randomly moving stimuli. Area MT is therefore able to determine the motion directions of several objects in the same space (Adelson & Movshon, 1982; Stoner & Albright,1992, 1996) and can segregate between objects and surfaces in a scene (Snowden, Treue, Erickson, & Andersen, 1991). This study determined that speed segmentation cues could also reduce processing time; however, speed also affected the perceived direction of motion.

Thus, motion processing combines speed and direction prior to global motion in area MT. This output is then forwarded to decision-making areas were color and speed segmentation reduced the processing time, providing evidence for ventral and dorsal information in the object representation (Perry et al., 2014).

It is important to note that in these studies spatial and feature-based attention can be ruled out to ensure that object-based attention is being studied. By having the two random dot kinetograms superimposed, the experiments controlled for spatial attention as both stimuli were in the same space. As well, the translations in the experiments occurred in the same eight directions for both surfaces and thus the attentional results are not due to the modulation of gain of motion channels associated with feature-based attention (Reynolds et al., 2003).

Thus far, we have seen that surfaces that are further separated from one another due to speed differences or spatial frequency allow for a reduction in processing speed as well as a more accurate perception of the direction. Thus, global motion processing happens with the integration of motion features: speed and direction in area MT (Perry et al., 2014). Afterward, color is integrated into the intermediate object representation after direction computation to allow for faster processing times to reach the decision threshold; therefore not affecting direction computations (Perry & Fallah, 2012). Similar to how the ventral stream integrates color with features from the dorsal stream to eventually lead to object recognition, the dorsal stream integrates features into the object files for decision-making processes.

EEG Components

Electroencephalography is a noninvasive technology that allows for brain activity to be recorded via electrodes placed on the scalp. A saline solution is added to the electrodes to allow electrical activity from the brain to be conducted through the electrodes, amplified, and recorded.

When neurons fire in the brain, ions are flowing across the cell membrane and thus causing electricity to be formed. The electroencephalogram (EEG) displays the changes in the voltage over time (Berger, 1929). EEG shows the coarse brain activity from the individual it is being used on. However, it is a useful technique as it can show what is occurring in the brain in real time and thus it has a high temporal resolution. As well, the recording is showing neural processes that are occurring in response to sensory, cognitive, and motor events in the environment. These responses are called event-related potentials (ERP). Event-related potentials can be used to determine the voltage changes in different areas of the brain as a result of a stimulus. The ERP data after filtering, amplification, artifact removal and averaging consists of positive and negative deflections, giving the wave characteristic deviations known as components. The first ERP component was described by Grey Walter in 1964 and it was named the contingent negative variation (Walter et al., 1964). In his experiment, Walter observed a consisted negative deflection in the ERPs in a time in the recording that suggested the negative voltage occurred when the participant was anticipating the stimulus. Afterward, many researchers began discovering different components that occur as a result of neural processing related to different events in experiments. The amplitude and latency of these components are used as measures of neural activity and cognitive processing.

The components important in this study are the P1, N1, P2, N2 and LPC components as they are associated with visual and attentional responses. The P1 component is the first clear positive deflection in the ERP signal and it is associated with spatial attention. The P1 component has the greatest amplitude at the lateral occipital electrodes, with a latency of 60-90ms post-stimulus with a peak between 100-130ms. However, these values vary depending on the contrast of the stimulus. The P1 component arises from the dorsal extrastriate cortex and a

later region of the component arises from the fusiform gyrus (Di Russo et al., 2002). The component amplitude and latency is affected by the stimulus parameters, direction of spatial attention, and the participant's state of arousal. The N1 component is the first clear negative deflection in the ERP signal following P1 and it is comprised of several subcomponents, all of which are associated with spatial attention and selective attention (Pinilla et al., 2001; Khoe et al., 2005). The N1 component has also been shown to be less responsive to a stimulus that is preceded by another stimulus in the same location (Luck et al., 1990). Studies have shown that the lateral occipital subcomponent of the N1 component is also associated with discriminative processing (Hopf et al., 2002; Ritter et al., 1979; Vogel & Luck, 2000), hence why it will be analyzed in this study. This subcomponent peaks at posterior electrode sites at 150-200ms poststimulus. Following the N1 component is the P2 component and it is associated with target features present in the stimulus. The P2 component is greatest at the anterior and central electrodes. Following the P2 component is the N2 component which is made up of several subcomponents. The N2pc subcomponent is associated with focal attention being placed on the target and possibly also the suppression of the items that are not the target (Eimer, 1996). It is largest contralateral to the target site and over the posterior sites. This component occurs during 200-300ms post-stimulus. Following the N2 component is the late positive component (LPC) associated with target probability. The amplitude of this component is largest when the probability of the target appearing becomes less as well as when the participants are trying harder to accomplish the task (Duncan-Johnson & Donchin, 1977; Israel et al., 1980). However, if the participant is unsure if the stimulus was the target or not, the LPC component decreases in amplitude.

EEG and Object-Based Attention

Using electroencephalography, Valdes-Sosa et al (1998) showed that neural responses to a brief translation were modulated by object-based attention. Their experiment consisted of two differently colored, superimposed, rotating RDKs where the baseline visual scene would allow the participant to either perceive two objects or one object in the visual display. When the two surfaces were rotating in the same direction, one surface was perceived. Whereas, when the two surfaces were rotating in opposite directions, two surfaces were perceived. Participants were told to attend to one rotating surface and report the direction of a brief translation of either the attended or unattended set of dots occurred. The brief translation causes event-related potentials associated with the translation *motion onset* (MO-ERPs). The MO-ERPs contain a P1/N1 component complex (Bach & Ullrich, 1994; Göpfert et al., 1990; Kuba & Kubová, 1992a and 1992b; Schlykowa et al., 1993) that was modulated by attention. They found a large suppression of the MO-ERPs' P1 and N1 components when the translation occurred on the unattended compared to the attended surface in the two perceived objects condition. In contrast, when the two fields of dots were rotating together and only one surface was perceived, the MO-ERPs' P1 and N1 components linked with the unattended dots were suppressed only moderately or not at all. Thus, in the two objects condition, participants were accessing the object file for the cued surface and suppressing the object file for the uncued surface resulting in suppression of the uncued P1/N1 components.

Attentional Capture

To engage object-based attention, Valdes-Sosa et al (1998) utilized an endogenous cue: they informed the participants which color dots would translate in advance of each trial. However, attention can also be allocated exogenously, or reflexively due to external events. Yantis and Jonides (1984; 1990) showed that the abrupt onset of a stimulus at a new location

draws attention to it over stimuli already present at other locations. Reynolds et al (2003) modified the Valdes-Sosa paradigm of superimposed surfaces to determine that an exogenous cue also allows for object-based selection when the surfaces were superimposed and could not be distinguished by spatial location. In this experiment, one of the two superimposed surfaces would appear first and rotate for 750ms before the second surface would appear and the two surfaces would rotate together. The second surface appearing later was an abrupt onset that cued the participant to that surface. They found that the delayed onset of one of the surfaces impaired processing of the other surface for hundreds of milliseconds. These results supported the biased competition model wherein the neurons representing the two surfaces automatically are in competition with each other but cueing one surface shifts the competition in its favor.

This is consistent with studies on monkeys with spatial attention where it has been shown that multiple stimuli appearing simultaneously in a visual field cause the activation of neurons in the extrastriate visual cortex and their competitive inhibition of each other. This occurs in dorsal stream (Recanzone & Wurtz, 2000; Recanzone et al., 1997) and ventral stream (Chelazzi et al., 1993; Luck et al., 1997; Reynolds et al., 1999). Fallah, Stoner, and Reynolds (2007) also showed a selective processing of stimuli in area V4 of the macaque. However, by using two distinctly colored superimposed surfaces and delaying the onset of one of the surfaces, they were able to show selective processing of the delayed surface and thus providing further evidence for surface-based or object-based selection. Thus, in Reynolds' study, the delayed onset of the second surface place the neurons at a competitive advantage and allow the participants to perform better when processing the translation direction of the cued surface and causing an impairment at processing the uncued surface.

While two superimposed dotfields produce transparent motion, the addition of the second moving pattern makes it harder to determine both patterns (e.g. Lindsey & Todd, 1998; Mather & Moulden, 1983; Snowden, 1989; Verstraten et al., 1996). This could be due the neurons in area MT that are directionally selective show reduced activity to a stimulus moving in the preferred direction in the presence of a second superimposed surface (Snowden et al., 1991; Qian & Andersen, 1994). As a result of mutual inhibition, the abrupt onset is an exogenous cue that causes this cued surface to dominate the neuronal responses and impair the competing neural responses for the uncued surface (Reynolds et al., 2003).

Chapter 2: Hypothesis

In this study, we modified the paradigm used previously (Valdes-Sosa et al 1998; Reynolds et al, 2003; Fallah, Stoner, & Reynolds, 2007) to determine behaviorally and electrophysiologically whether additional distinguishing object features would strengthen object-based selection. Two superimposed, rotating RDKs were used with one surface having a delayed surface to be used as a cue. At varying time points, there was a brief translation of either the cued or uncued surface before the two surfaces returned to rotating. In half of the trials, the two surfaces were the same color and in the other half of the trials the two surfaces were different colors. First, we tested whether exogenous cueing would affect early motion onset components P1/N1, similar to endogenous selection, seen in the P1/N1 complex in the study by Valdes-Sosa et al (1998). Furthermore, if selection of superimposed surfaces in the dorsal stream is dependent on object files, we expect that color differences should increase the suppression of the uncued surface versus when the two surfaces were the same color due to the additional distinguishing feature of color strengthening the surface selection. In addition, we may be able to determine if binding occurs in the occipital (visual processing) versus parietal (information accumulation - decision-making) versus prefrontal (decision-making) areas of the brain.

Chapter 3: Manuscript

Preface

Object-based selection refers to the grouping of information in such a way that the groups correspond to discrete objects. Gestalt properties of spatial proximity, continuity of contour, shared color or movement are used to segregate objects from one another at which point they can be focally attended to (Duncan, 1984). We investigated whether object-based selection is modulated by the strength of the object representations. Using two superimposed surfaces that control for spatial attention, we tested whether an additional distinguishing feature would increase the suppression of the unattended surface. We expected that when the surfaces were segregated by color, the combination of color and motion as distinguishing features would produce an object file with a stronger representation in the brain. This would lead to a greater suppression of the uncued surface in comparison to when the two surfaces are of the same color. We found a greater cueing effect when the surfaces differed in color compared to when they were the same color. We then investigated the event related potentials (P2, N2, P3 components) in the parietal and frontal regions of the brain to describe the underlying mechanisms subserving object-based selection.

Introduction

Understanding how features processed separately are integrated into a common object representation in the brain is one of the grand challenges remaining in neuroscience. Features are bound from within and across the ventral and dorsal visual streams. Feature integration theory (FIT) posits that features of an object are processed first and are then bound by spatial location to form an *object file* and compared to stored representations to identify the object (Treisman et al.,

1977). Marr (1982) described a similar concept using his visual theory. He described the brain initially forming a primal sketch, the 2D sketch, before forming a 2.5D intermediate sketch, and finally forming a 3D model providing object recognition. The intermediate object file from FIT is thought to be an analog of Marr's 2.5D sketch. Further, Nakayama et al. (1995) have suggested that intermediate object representations are the substrate for object-based attention. They suggest that object-based attention selects surfaces, which are intermediate object representations produced by combining the initial features of the object but before more complex visual processing such as a 3D representation and object recognition.

There is strong evidence for object-files in the ventral stream (Mitroff et al., 2005, 2007, 2009; Noles et al., 2005). Studies showing cross-talk between the dorsal and ventral streams (Schiller, 1993; Sereno & Maunsell, 1998; Tsutsui et al., 2001; Sereno et al., 2002; Peuskens et al., 2004; Durand et al., 2007; Lehky & Sereno, 2007; Wannig et al., 2007; Konen & Kastner, 2008; Tchernikov & Fallah, 2010; Perry & Fallah, 2012) support the existence of object files in the dorsal stream (Perry et al., 2014; for review see Perry & Fallah, 2014), which can also include ventral stream features (e.g. color: Tchernikov & Fallah, 2010; Perry & Fallah, 2012; 2014). However, dorsal stream object files do not give rise to object recognition as in the ventral stream.

In a study by Perry and Fallah (2012), cross-stream feature integration was shown through the ventral stream feature of color speeding up the processing of a dorsal stream feature: direction of motion. Next, Perry et al. (2014) determined that surfaces distinguished by an additional dorsal stream feature: speed of motion, also reduced processing time; however, speed also improved the perceived direction of motion. Thus, global motion processing is based upon the integration of motion features: speed and direction in area MT (Perry et al., 2014).

Afterward, color is integrated into the intermediate object representation after direction computation to allow for faster processing times to reach the decision threshold (Perry & Fallah, 2012). Similar to how the ventral stream integrates features from the dorsal stream to eventually lead to object recognition in structure-from-motion stimuli (Johansson, 1973, 1976; Siegel & Andersen, 1988), the dorsal stream integrates features into the object files for decision-making processes about motion perception.

Using electroencephalography, Valdes-Sosa et al (1998) showed that neural responses to a brief translation were modulated by object-based attention. Their experiment consisted of two differently colored, superimposed, rotating RDKs where the baseline visual scene would allow the participant to either perceive two objects or one object in the visual display. Participants were told to attend to one of the sets of rotating dots and at some point, a brief translation movement of either the attended or unattended set of dots occurred. The brief translation causes event-related potentials associated with the translation *motion onset* (MO-ERPs). The MO-ERPs contain a P1/N1 component complex (Bach & Ullrich, 1994; Göpfert et al., 1990; Kuba & Kubová, 1992a and 1992b; Schlykowa et al., 1993) that was modulated by attention. They found that in the two objects condition, participants were accessing the object file for the cued surface and suppressing the object file for the uncued surface resulting in suppression of the uncued P1/N1 components.

While Valdes-Sosa et al (1998) utilized an endogenous cue (they informed the participants which color dots would translate in advance of each trial), attention can be allocated exogenously, or reflexively due to external events. Yantis and Jonides (1990) showed that abrupt onset of a stimulus at a new location draws attention to it over stimuli already present at other locations. Reynolds et al (2003) modified the Valdes-Sosa paradigm of superimposed surfaces to

determine that an exogenous cue also allows for object-based selection when the surfaces were superimposed and could not be distinguished by spatial location. They found that the delayed onset of one of the surfaces impaired processing of the other surface for hundreds of milliseconds. These results supported the biased competition model wherein the neurons representing the two surfaces automatically are in competition with each other but cueing one surface shifts the competition in its favor.

In this study, we modified the object-based attention paradigm used previously by Valdes-Sosa et al (1998), Reynolds et al (2003), and Fallah, Stoner, & Reynolds, (2007). Two superimposed, rotating RDKs were used with one surface having a delayed onset as an exogenous cue. At varying time points, there was a brief translation of either the cued or uncued surface before returning to rotation. In half of the trials, the two surfaces were the same color and in the other half of the trials the two surfaces were different colors. First, we tested whether exogenous cueing could affect early motion onset components P1/N1, similar to the effects of top-down endogenous selection, seen in the P1/N1 complex (Valdes-Sosa et al, 1998). Furthermore, if selection of superimposed surfaces in the dorsal stream is dependent on object files, we expect that color differences should increase the suppression of the uncued surface versus when the two surfaces were the same color, reflected both in accuracy and in the ERP components. In addition, The P2, N2, P3 components (associated with visual and attentional responses) were analyzed in the parietal and frontal regions of the brain to determine if dorsal-stream binding occurs in the occipital (visual processing) versus parietal (information accumulation - decision-making) versus prefrontal (decision-making) areas of the brain.

Methods

Participants

Twenty-eight university students participated in this experiment (20-43 yrs; 13 male and 15 female; 2 left-handed). All participants had normal or corrected-to-normal visual acuity and none tested positive for color blindness using Isihara plates. Informed consent was obtained from all participants and the research was approved by York University's Human Research Participant Committee.

Apparatus

Experiments were conducted in a dark, quiet, and electrically shielded room. Stimuli were presented on a computer monitor (21" ViewSonic, 1024x768x32 resolution, 60Hz) placed 57 cm from the participants. A chinrest stabilized head position. A desk-mounted infrared eye tracker (ISCAN Inc) monitored the right eye position. Electroencephalogram (EEG) data was acquired using the Neuroscan SynAmps and Quik-Caps system (Compumedics, Inc). Participants were instructed to minimize body movements and eye blinks during EEG recording. Stimuli were created using Matlab (The Mathworks Corp.) and experimental control was accomplished using Presentation software (Neurobehavioural Systems). Photometric isoluminance for all stimuli was determined using a photometer (PR-655, Photo Research Inc.). EEG data was analyzed using EEGlab (SCCN) and SPSS (SPSS Inc).

Experimental Paradigm

The stimuli consisted of two overlapping random dot kinematograms (RDK) on a black background. The two dot fields rotated in opposite directions and were of photometrically equiluminant colors (CIE - red: x=0.64, y=0.33; green: x=0.29, y=0.60; isoluminant, 24.4cd/m^2). The two surfaces were both red for 25% of the trials, both green for 25% of the trials, and one red, one green for 50% of the trials. Each dot was 0.038dva, and rotated at a speed of 5°/sec.

Each RDK was 14dva in diameter with a dot density of 2.6 dots/deg^2. A trial was initiated with the appearance of a white marker in the center of the screen that the participant fixated on throughout the stimulus presentation. If fixation was broken before the end of the trial, the trial was aborted and randomly reinserted into the remaining trials. After 200ms, the centrally located stimulus appeared on the screen. Initially, one of the RDKs appeared alone for 350ms, 383ms, or 416ms before the second RDK appeared. The first RDK was either red or green and rotated either clockwise or counterclockwise. The selection of this RDK was random and with equal probability. The second surface then appeared in order to allow for an abrupt onset that automatically cued the participant's attention to the second surface (Jonides & Yantis, 1988). The second RDK was either red or green and rotated in the opposite direction of the first surface. The two surfaces continued to rotate together for another 350ms, 383ms, or 416ms after which, 60% of the dots of one of the surfaces (cued or uncued) transformed from rotation to translation on the next screen refresh while the other set of dots continued to rotate. After 150ms, the translational dots returned to their original rotation direction on the following screen refresh and both surfaces continued rotating for 550ms (see Figure 1). During translational motion, the dots moved in one of eight directions (0º, 45º, 90º, 135º, 180º, 225º, 270º and 315º) at a speed of 5º/sec. The variation in duration of RDK's produced three stimulus onset asynchronies for both the abrupt onset of the second RDK and the onset of the translation, resulting in nine variations in timing (1400-1600ms) to reduce expectation alpha in the EEG signal. Once the stimulus disappeared, the participants indicated the direction of translation using a number pad with eight directional keys. Accuracy was emphasized over speed.

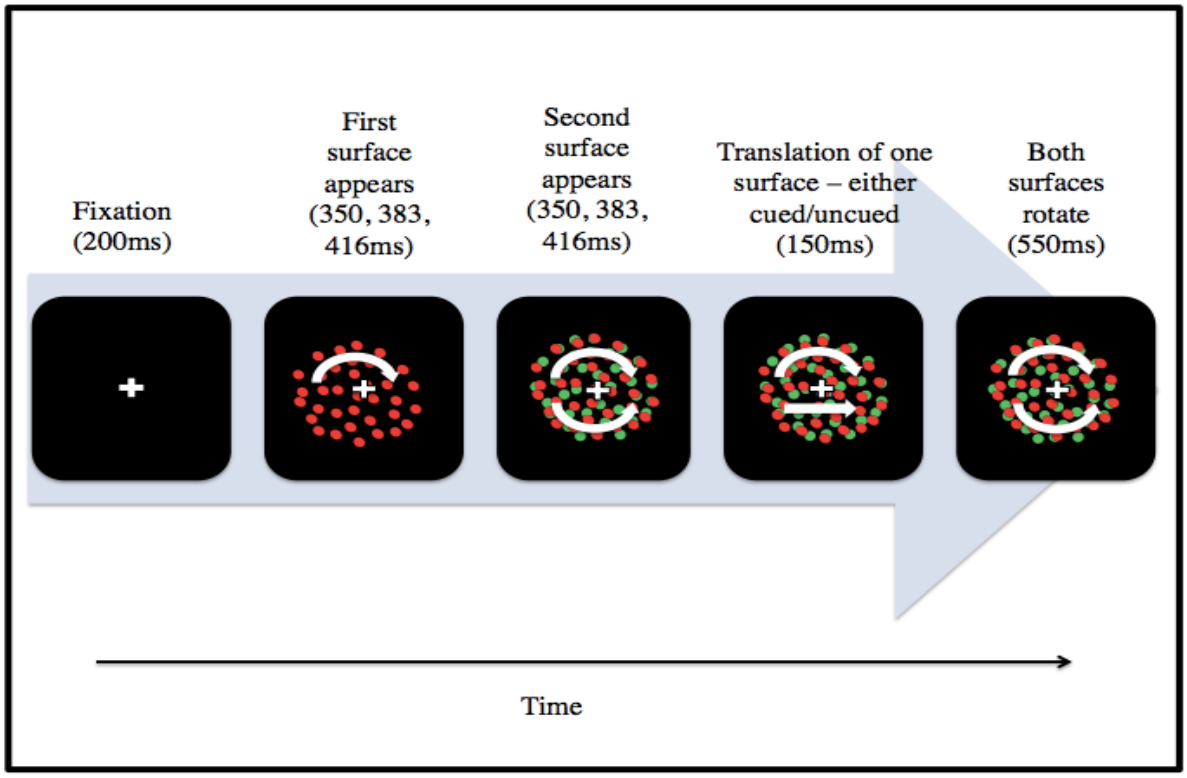

Figure 1: Study Stimulus. Representation of the stimulus material for an uncued bicolor condition trial.

Design

This study consisted of a 2x2 factorial design for color (bicolor and unicolor) and cueing (cued and uncued surface). In addition, in the bicolor condition, there were eight possible translational motion directions, two rotation directions (clockwise and counterclockwise), as well as three stimulus onset asynchronies (SOAs) for the abrupt onset and the translational motion, for a total of nine possible SOA conditions. This gave a total of 576 possible stimulus combinations for the bicolor stimuli. There were also 576 possible combinations in the unicolor condition. 2 colors (red or green) x 2 cueing conditions (cued and uncued) x 2 surface rotations (clockwise and counterclockwise) x 8 translational motion directions x 3 abrupt onset SOAs x 3

translational motion SOAs. Each block consisted of 20 unicolor and 20 bicolor trials. The unicolor trials were randomly selected from the array of 576 unicolor movies and the bicolor trials were randomly selected from an array of 576 bicolor movies. There were 20 blocks in total to give 800 trials per collection. There was a practice block prior to the beginning of the 20 blocks to ensure the participant understood the instructions. Participants were able to rest in between blocks.

Electrophysiology

A 64-channel Quick-Cap was used with an additional four electrodes to record the electroculogram (EOG). The impedance between the scalp and electrodes was brought down below 5kΩ using saline solution. In each trial, timestamps corresponding to stimulus events [abrupt onsets and linear motion-onsets (MO-ERPs)] were co-registered with the amplified and digitized EEG signals.

Off-line analysis was performed using EEGlab. Preprocessing consisted of down-sampling the data from 1000Hz to 250Hz, Butterworth filtering between 0.1 and 50 Hz, removing practice and incorrect trials, and separating the remaining data into the various conditions. Gross artifacts (i.e. muscle (EMG) movements), ocular (EOG) movements, and other activity from artifactual sources were removed using ADJUST and ICA. On average 4 poor channels per participant were interpolated. The data was then epoched with a prestimulus baseline of 100ms before pattern onset and 700ms poststimulus epoch. Afterward, all active electrodes were referenced to electrode Cz. For every subject, average ERPs time-locked to the onset of translation motion were obtained for each stimulus condition. A low pass IIR Butterworth filter with a half-amplitude cutoff at 30 Hz and roll-off slope of 12 dB/octave was run on the data. Following this, a grand average across all the participants was performed.

The mean amplitude in microvolts of the ERP components were measured for the components P1, N1, P2, N2, and P3. The time windows were defined as 80ms-150ms (P1/N1) for the occipital electrodes, 200ms-400ms (P2/N2/P3) for the parietal electrodes, and 250ms-450ms (P2/N2/P3) for the frontal electrodes. The average prestimulus voltage was subtracted from the measurement window voltage. The grand average for the ERPs across all sessions was used to compute the mean amplitude for each site and condition.

Analysis

We first analyzed the behavioral responses by performing a 2 (cued vs uncued) X 2 (unicolor vs bicolor) rm-ANOVA on the accuracy of detecting the translation direction. Similar ERP analyses were conducted using the mean amplitude measurements of the P1, N1, P2, N2, and P3 components taken for occipital, parietal, and frontal electrodes. The electrodes observed were consistent with what has been shown to be used in previous ERP literature using the 10/20 EEG system. In the ERP analyses, hemisphere (medial/lateral location) and line (anterior/posterior location) were taken into consideration in a manner consistent with what is currently performed in ERP research. Both behavioral and ERP analysis were conducted originally to include all twenty-eight participants and subsequently to only include the eighteen participants that met the accuracy criteria of 50% and above. The Greenhouse-Geisser procedure was used when the rm-ANOVA sphericity assumption was violated.

Results

All participants

Behavioral Results

The mean accuracy rate for each condition was as follows: bicolored cued 59.6% (SEM=3.0), bicolor uncued 48.9% (SEM=3.0), unicolor cued 59.5% (SEM=3.1), and unicolor uncued 55.0% (SEM=2.9). A 2x2 factorial ANOVA was conducted comparing the conditions. There was a significant main effect of Color ($F(1,81)=8.0$, $p=0.009$), a significant main effect of Cueing ($F(1,81)=21.8$, $p<0.001$), and a significant Color X Cue interaction ($F(1,81)=8.0$, $p=0.009$) (see Figure 2).

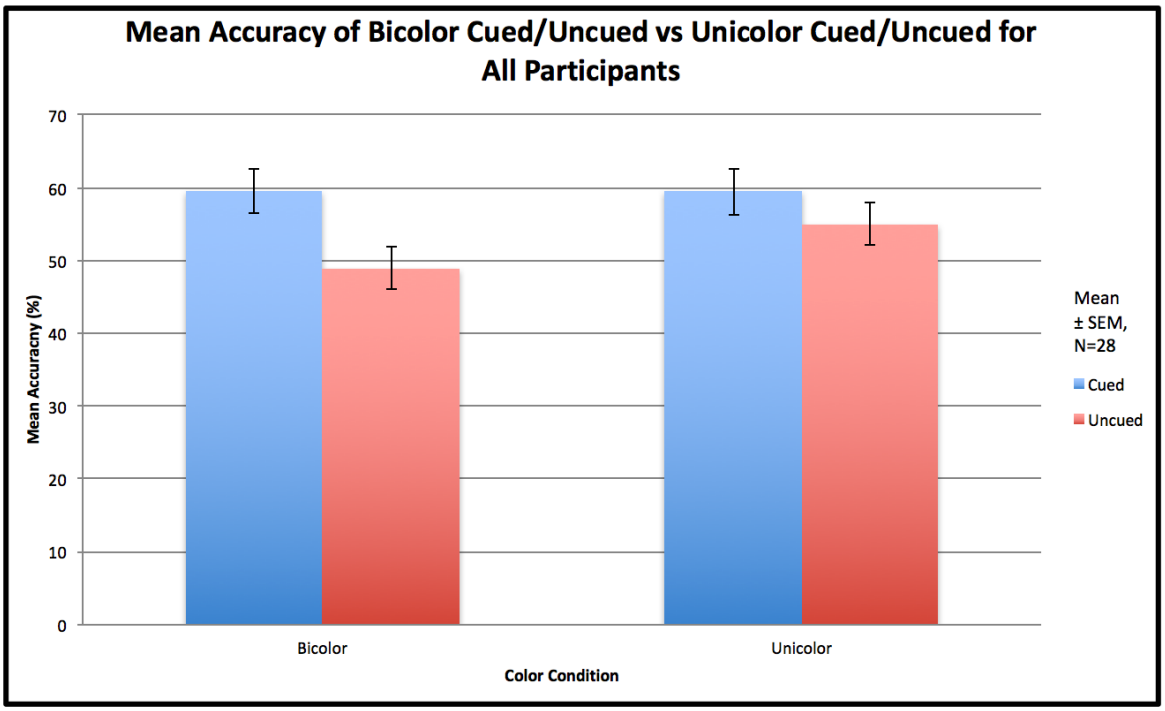

Figure 2: Behavioral Effects across all Conditions. Bar graphs of the behavioral analysis showing the mean accuracy percentage for the bicolor cued, bicolor uncued, unicolor cued, and unicolor uncued conditions for all participants.

A Bonferroni post-hoc analysis was performed to determine the nature of the cueing effect based on whether the surfaces were the same or different colors. When the surfaces were bicolored, there was a significant mean difference of 10.7% (SEM=0.4) between the cued and

uncued conditions ($F(1,27)=22.2$, $p<0.001$. When the surfaces were the same color, there was a significant mean difference of 4.5% (SEM= 0.3) between the cued and uncued conditions ($F(1,27)=8.2$, $p=0.008$) (see Figure 3). Thus the cueing effect was larger in the bicolored than the unicolored condition (Cue X Color interaction).

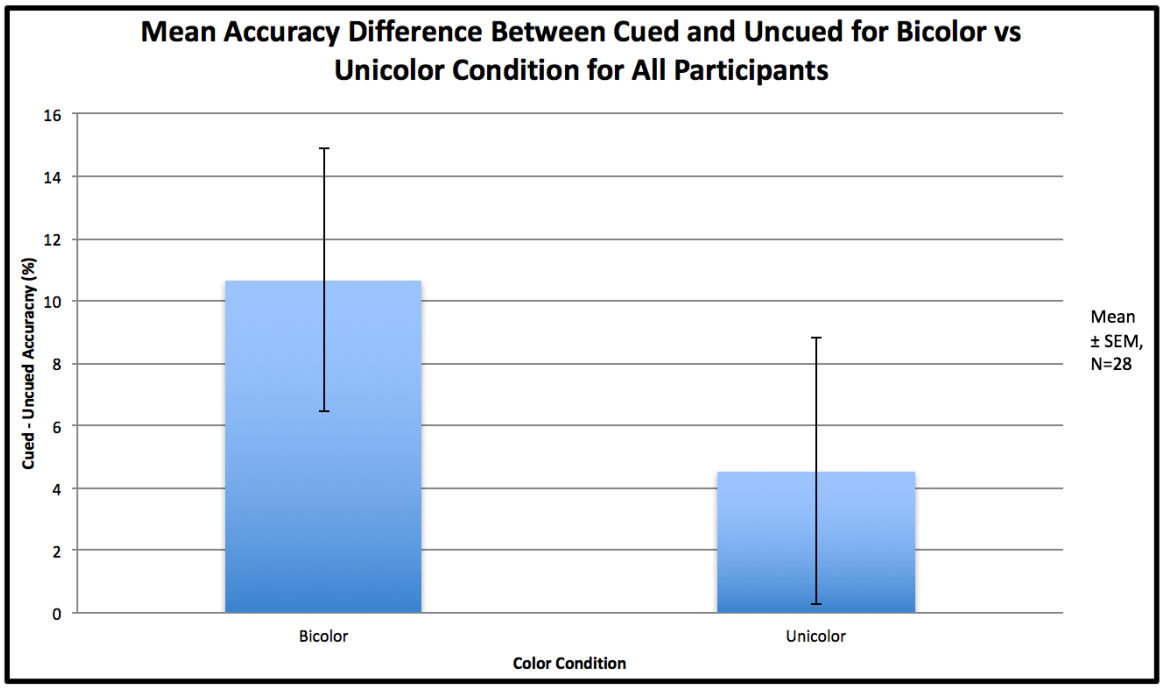

Figure 3: Behavioral Cueing Effect per Color. Bar graphs of the behavioral analysis showing the mean accuracy difference between the cued and uncued conditions in the bicolor and unicolor conditions for all participants.

Event Related Potential (ERP) Results

For the occipital electrodes a 2(color) x 2(cue) x 2(hemisphere) mixed design ANOVA was performed to determine if there was a larger component suppression for the uncued surface compared to the cued surface for the bicolor versus unicolor conditions. Hemisphere was a factor used to compare the electrodes on the left side of the scalp to those on the right side of the scalp. The results for the occipital electrodes provided no evidence for a significant main effect of color

($F(1,81)=0.4$, $p=0.548$) or cue ($F(1,81)=3.1$, $p=0.088$). Furthermore, the results provided no evidence for a significant interaction between color and cue ($F(1,81)=0.6$, $p=0.431$) or color, cue, and hemisphere ($F(1,81)=0.1$, $p=0.744$).

For the parietal electrodes, a 2(color) x 2(cue) x 2(line) x 4(hemisphere) mixed design ANOVA was performed to determine if there was a larger component suppression for the uncued surface compared to the cued surface for the bicolor versus unicolor conditions. Line was a factor used to compare the electrodes that are positioned anteriorly to those positioned posteriorly. Hemisphere was a factor used to compare electrodes placed farthest left, inner left, inner right, and farthest right on the scalp. The results for the parietal electrodes showed that there was a significant main effect of color ($F(1,81)=4.6$, $p=0.041$) (see Figure 4). The results provided no evidence for a significant main effect of cue ($F(1.81)=3.3$, $p=0.079$), a significant interaction between color and cue ($F(1,81)=0.8$, $p=0.388$), or a significant interaction between color, cue, line, and hemisphere ($F(1,81)=2.0$, $p=0.152$).

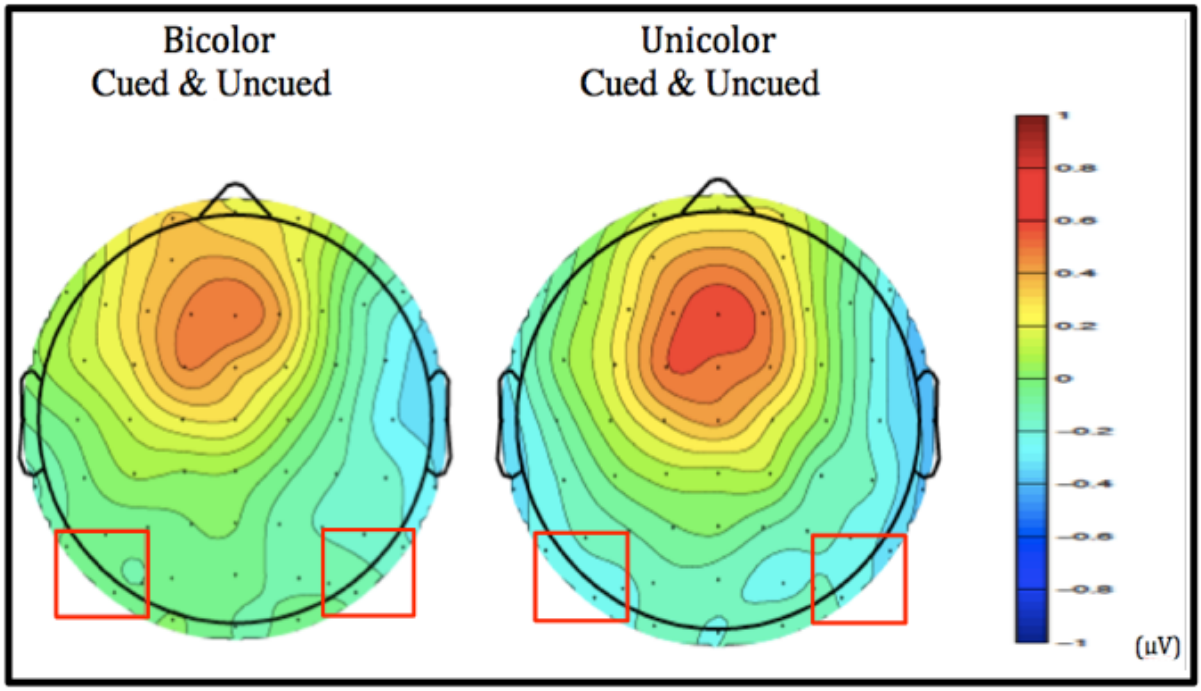

Figure 4: Main Effect of Color. Scalp maps for parietal electrodes (P7, P5, P6, P8, PO7, PO5,

PO6, & PO8) showing the voltage change for the bicolor cued & uncued and unicolor cued & uncued conditions occurring at mean amplitude for 200ms to 400ms for all participants.

For the frontal electrodes a 2(color) x 2(cue) x 2(line) x 3(hemisphere) mixed design ANOVA was performed to determine if there was a larger component suppression for the uncued surface compared to the cued surface for the bicolor versus unicolor conditions. Line was a factor used to compare the electrodes that are positioned anteriorly to those positioned posteriorly. Hemisphere was a factor used to compare electrodes placed left of midline, on midline, and right of midline on the scalp. The results for the frontal electrodes provided no evidence for a significant main effect of color ($F(1.6,81)=2.7$, $p=0.109$) or cue ($F(1.6,81)=3.6$, $p=0.069$). Furthermore, the results provided no evidence for a significant interaction between color and cue ($F(1.6,81)=0.1$, $p=0.76$) or significant interaction between color, cue, line, and hemisphere ($F(1.6,81=0.6$, $p=0.499$).

Performance-based analysis

Performance varied greatly across the conditions as follows: bicolor cued: 30.2 – 82.9%, bicolor uncued: 21.7 – 88.5%, unicolor cued: 33.7 – 86.4%, and unicolor uncued: 27.7 – 88.1%. Due to this, we focused on participants who could perform the task by correctly determining the translation direction of both the bicolor cued and unicolor cued conditions at least 50% of the time (chance: 12.5%). The18 participants (20-43 yrs; 7 male and 11 female; 1 left-handed) that fit into these criteria had their behavioral and EEG data re-analyzed.

Behavioral Results

The mean accuracy rate for each condition was as follows: bicolor cued 68.6% (SEM=2.2), bicolor uncued 55.7% (SEM=3.3), unicolor cued 69.2% (SEM=2.8), unicolor

uncued 63.0% (SEM=2.9). A 2x2 factorial ANOVA was conducted comparing the conditions. There was a significant main effect of Color ($F(1,51)=8.6$, $p=0.009$), and Cueing ($F(1,51)=23.0$, $p<0.001$), and a significant Color X Cue interaction ($F(1,51)=6.9$, $p=0.018$) (see Figure 5).

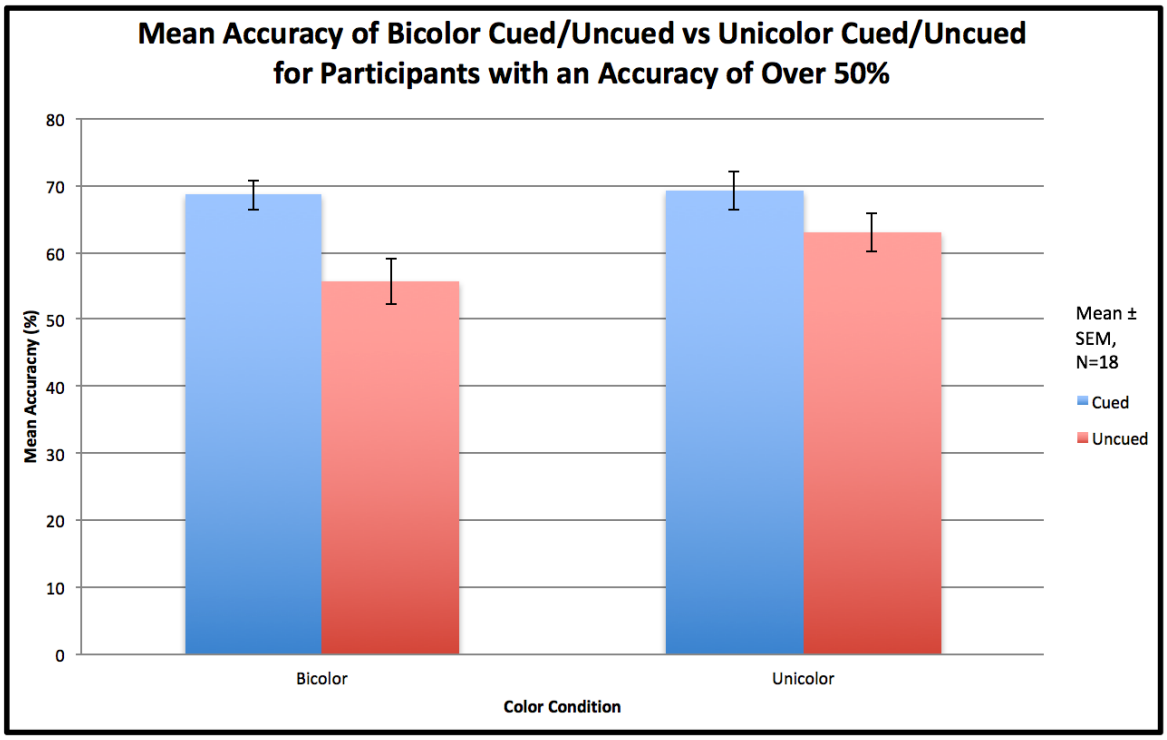

Figure 5: Behavioral Effects across all Conditions. Bar graphs of the behavioral analysis showing the mean accuracy percentage for the bicolor cued, bicolor uncued, unicolor cued, and unicolor uncued conditions for participants with over 50% accuracy.

A Bonferroni post-hoc analysis was performed to determine the cueing effect within the bicolored and unicolored conditions. When the surfaces were bicolored, there was a significant mean difference of 12.936% (SEM=0.608) between the cued and uncued conditions ($F(1,17)=25.2$, $p<0.001$). When the surfaces were the same color, there was a significant mean difference of 6.213% (SEM= 0.506) between the cued and uncued conditions ($F(1,17)=8.382$,

p=0.010) (see Figure 6). Therefore, the cueing effect was larger when the surfaces differed in color than when they were the same color.

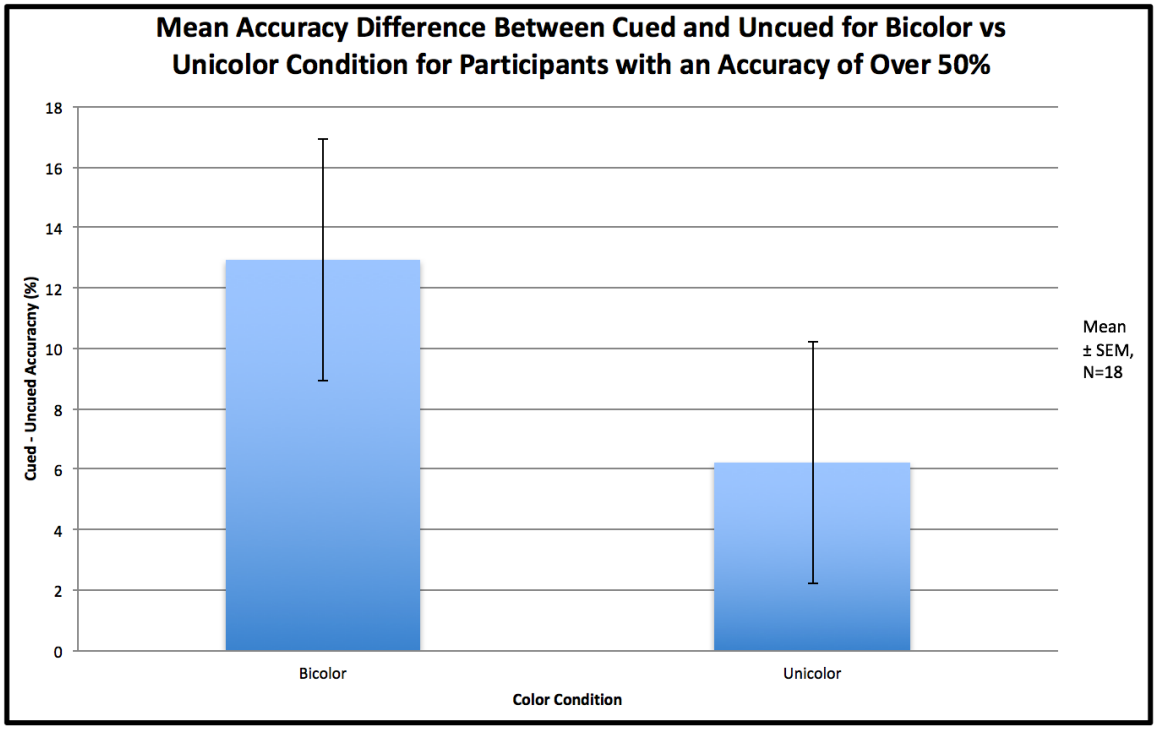

Figure 6: Behavioral Cueing Effect per Color. Bar graphs of the behavioral analysis showing the mean accuracy difference between the cued and uncued conditions in the bicolor and unicolor conditions for participants with over 50% accuracy.

Event Related Potential (ERP) Results

For the occipital electrodes, the 2(color) x 2(cue) x 2(hemisphere) mixed design ANOVA provided no evidence of any main effects or significant interaction between color, cue, and hemisphere (F(1,51)=0.8, p=0.380). Two 2(cue) x 2(hemisphere) mixed design ANOVAs were conducted to compare the cued and uncued conditions within each color condition. The results showed a significant cueing effect within the bicolor condition (F(1,17)=8.8, p=0.009) (see

Figure 7), but provided no evidence of a significant cueing effect within the unicolor condition ($F(1,17)=1.2$, $p=0.297$) (see Figures 8 & 9).

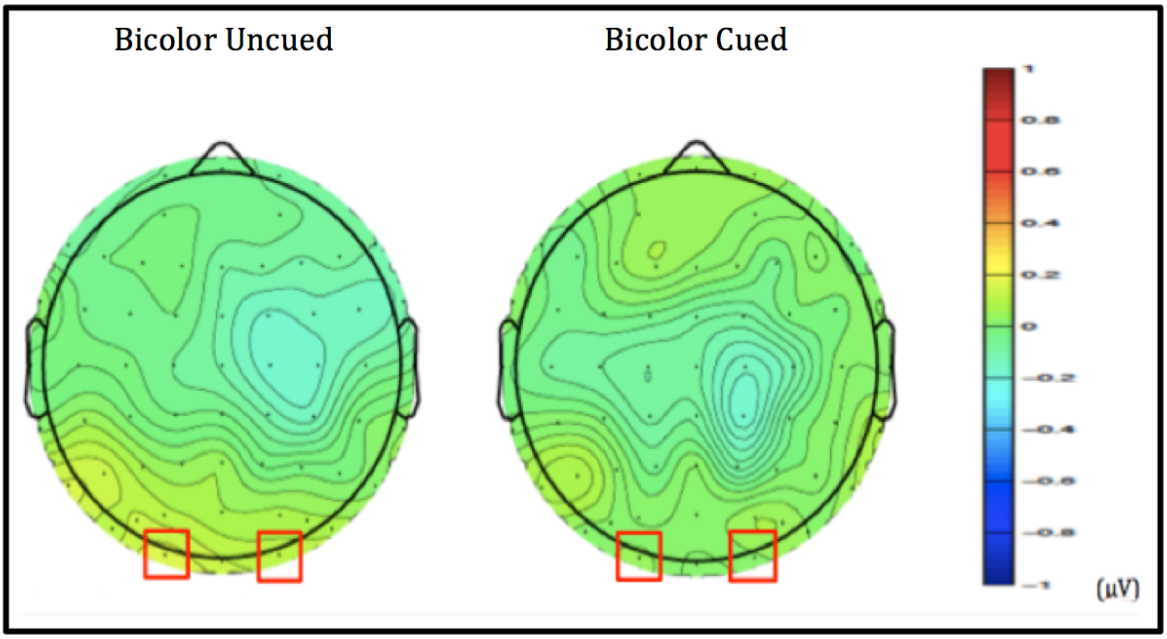

Figure 7: Cueing Effect in the Bicolor Condition. Scalp maps for occipital electrodes (O1 & O2) showing the voltage change for the bicolor cued and bicolor uncued conditions occurring at mean amplitude of 80ms to 150ms for participants with an accuracy rate of over 50%.

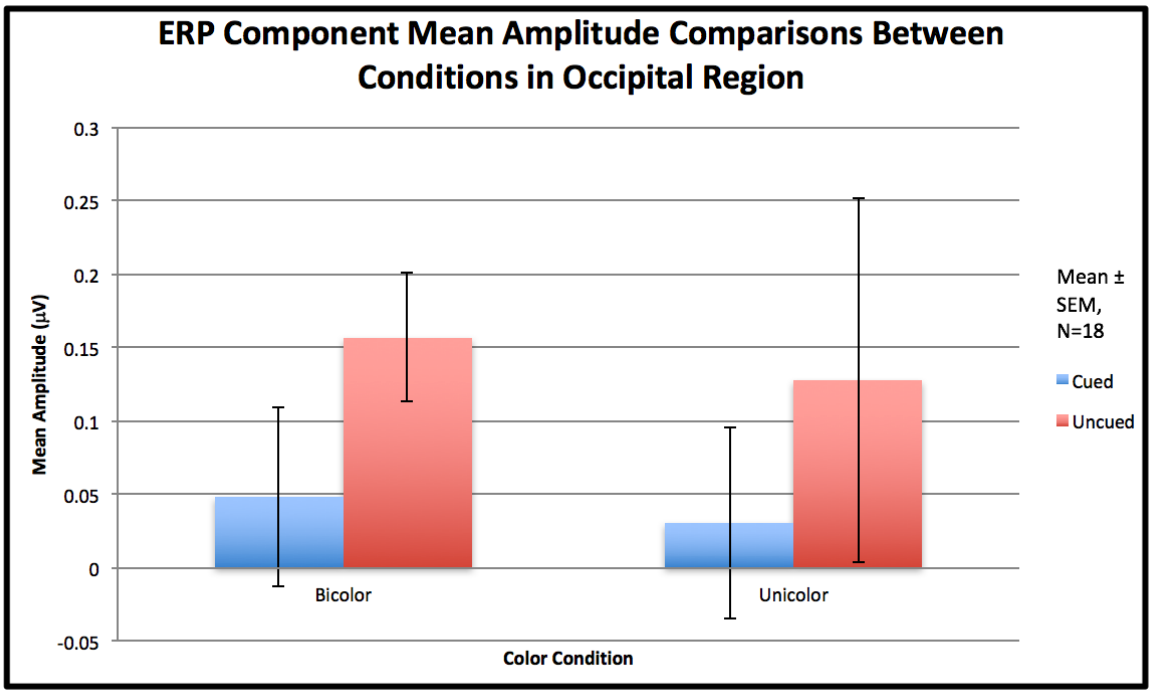

Figure 8: ERP Amplitudes across all Conditions. Bar graphs showing the mean amplitude in μV for the bicolor cued, bicolor uncued, unicolor cued, and unicolor uncued conditions in occipital electrodes (O1 & O2) occurring at 80ms to 150ms for participants with an accuracy rate of over 50%.

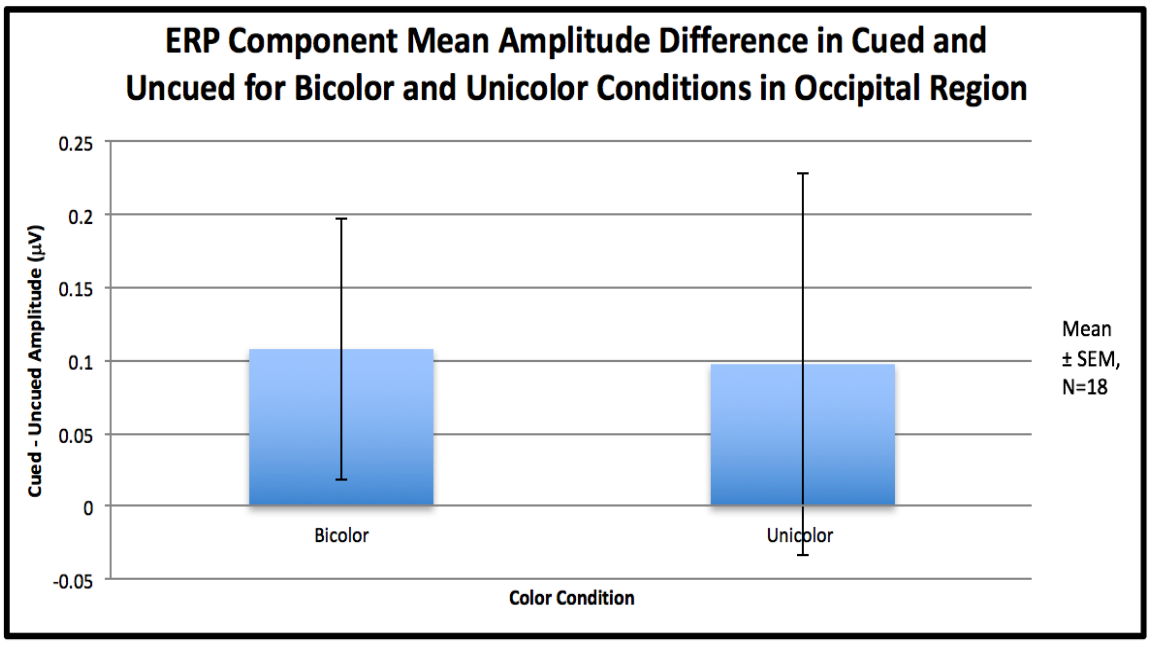

Figure 9: ERP Cueing Effect per Color. Bar graphs showing the mean amplitude difference in μV between the cued and uncued conditions for the bicolor and unicolor conditions in occipital electrodes (O1 & O2) occurring at 80ms to 150ms for participants with an accuracy rate of over 50%.

For the parietal electrodes, the 2(color) x 2(cue) x 2(line) x 4(hemisphere) mixed design ANOVA showed a significant cueing effect ($F(1,51)=11.0$, $p=0.004$) (see Figure 10) and a significant color, line and hemisphere interaction ($F(2.2,51)=3.6$, $p=0.035$) (see Figure 11), but none of the cueing by color interactions were significant.

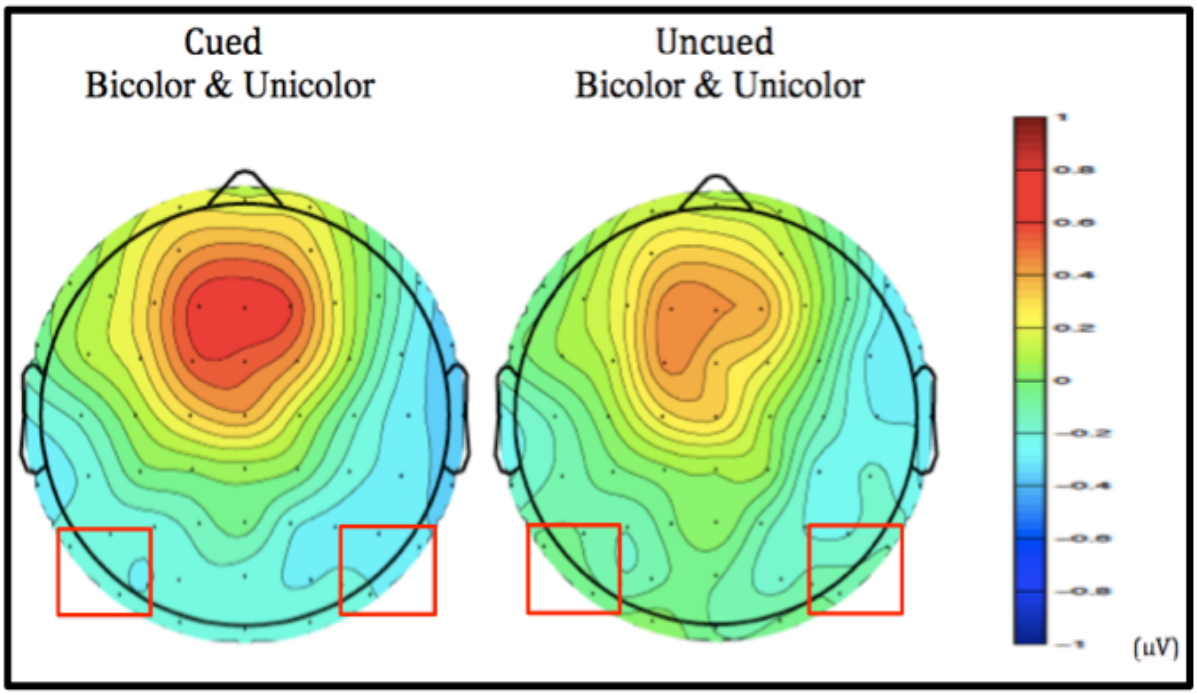

Figure 10: Main Effect of Cueing. Scalp maps for parietal electrodes (P7, P5, P6, P8, PO7, PO5, PO6, & PO8) showing the voltage change for the cued bicolor & unicolor and uncued bicolor & unicolor conditions occurring at mean amplitude of 200ms to 400ms for all participants with an accuracy rate of over 50%.

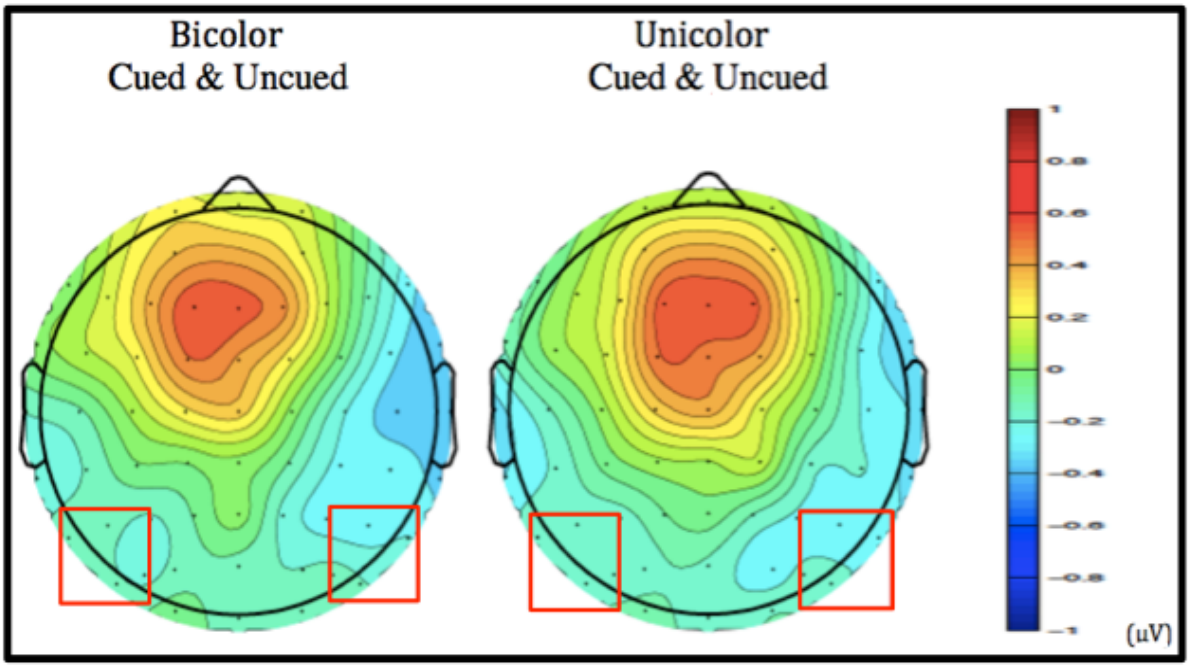

Figure 11: Main Effect of Color. Scalp maps for parietal electrodes (P7, P5, P6, P8, PO7, PO5, PO6, & PO8) showing the voltage change for the bicolor cued & uncued and unicolor cued & uncued conditions occurring at mean amplitude of 200ms to 400ms for all participants with an accuracy rate of over 50%.

Two 2(cue) x 2(hemisphere) mixed designed ANOVAs were conducted to compare the cued and uncued conditions within each color condition. The results showed a significant cueing effect within the bicolor condition ($F(1,17)=4.8$, $p=0.042$) (see Figure 12), but provided no evidence of a significant cueing effect within the unicolor condition ($F(1,17)=4.1$, $p=0.060$) (see Figures 13 & 14).

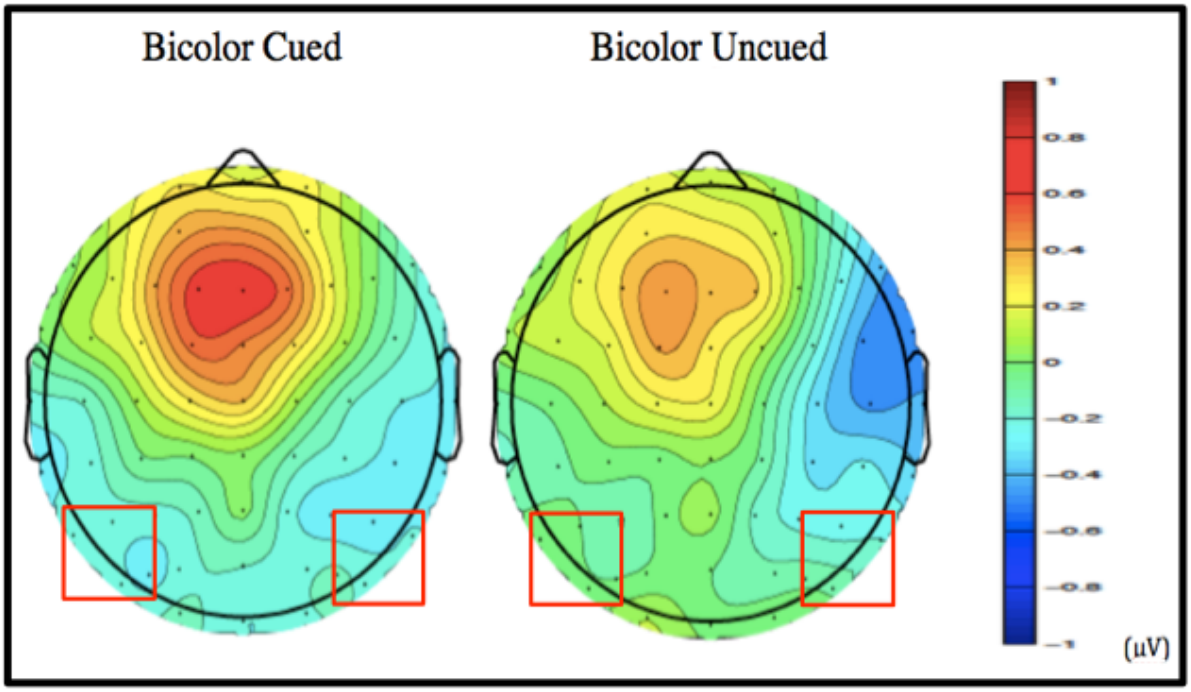

Figure 12: Cueing Effect in the Bicolor Condition. Scalp maps for parietal electrodes (P7, P5, P6, P8, PO7, PO5, PO6, & PO8) showing the voltage change for the bicolor cued and bicolor uncued conditions occurring at mean amplitude of 200ms to 400ms for all participants with an accuracy rate of over 50%.

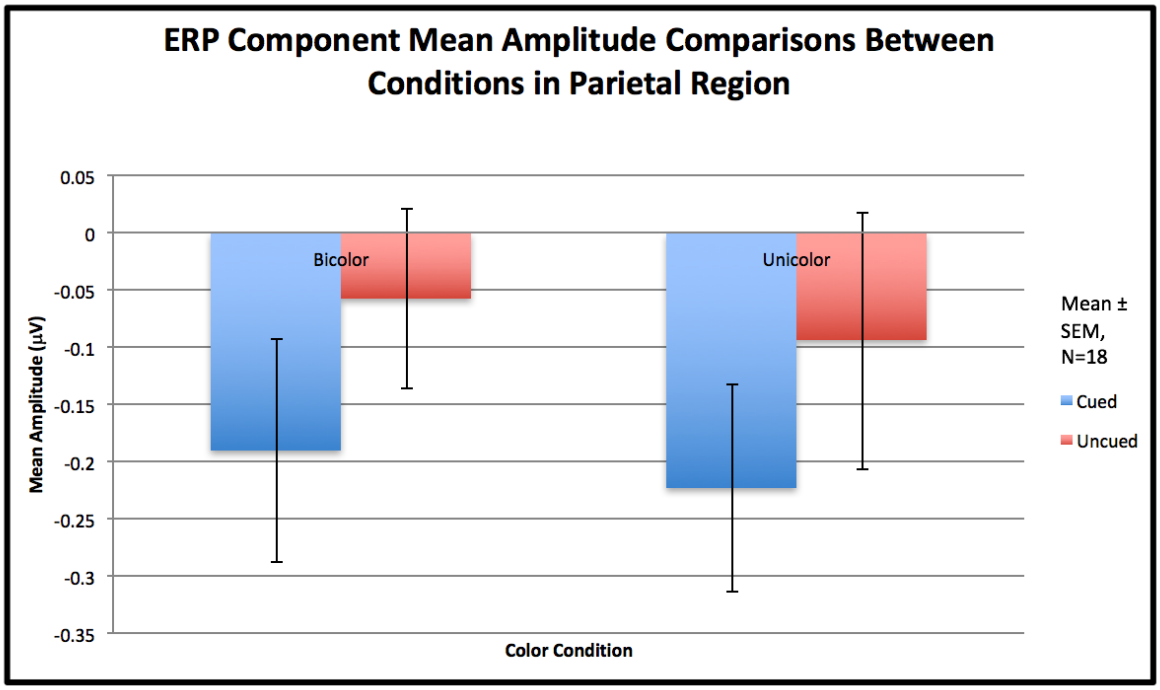

Figure 13: ERP Amplitudes across all Conditions. Bar graphs showing the mean amplitude in μV for the bicolor cued, bicolor uncued, unicolor cued, and unicolor uncued conditions in parietal electrodes (P7, P5, P6, P8, PO7, PO5, PO6, & PO8) occurring at 200ms to 400ms for participants with an accuracy rate of over 50%.

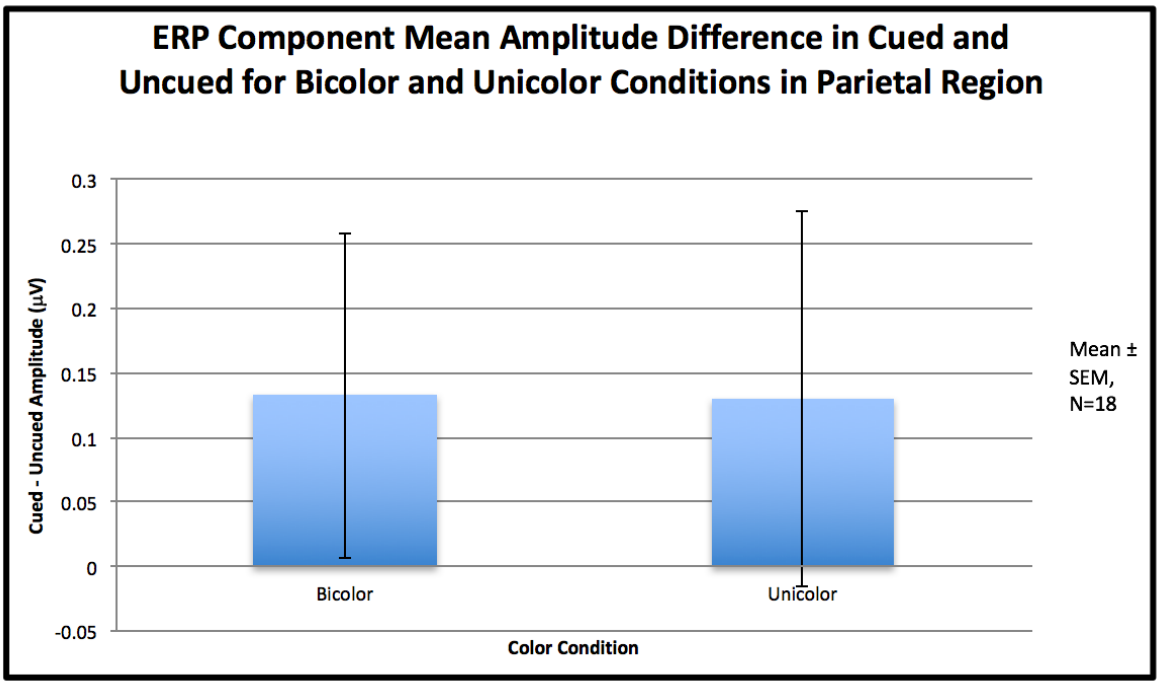

Figure 14: ERP Cueing Effect per Color. Bar graphs showing the mean amplitude difference in μV between the cued and uncued conditions for the bicolor and unicolor conditions in parietal electrodes (P7, P5, P6, P8, PO7, PO5, PO6, & PO8) occurring at 200ms to 400ms for participants with an accuracy rate of over 50%.

For the frontal electrodes, the 2(color) x 2(cue) x 2(line) x 3(hemisphere) mixed design ANOVA showed a significant cueing effect ($F(1,51=10.2$, $p=0.005$) (see Figure 15), a significant color and line interaction ($F(1,51=5.7$, $p=0.029$), and significant color and hemisphere interaction ($F(1,51=5.6$, $p=0.013$) (see Figure 16).

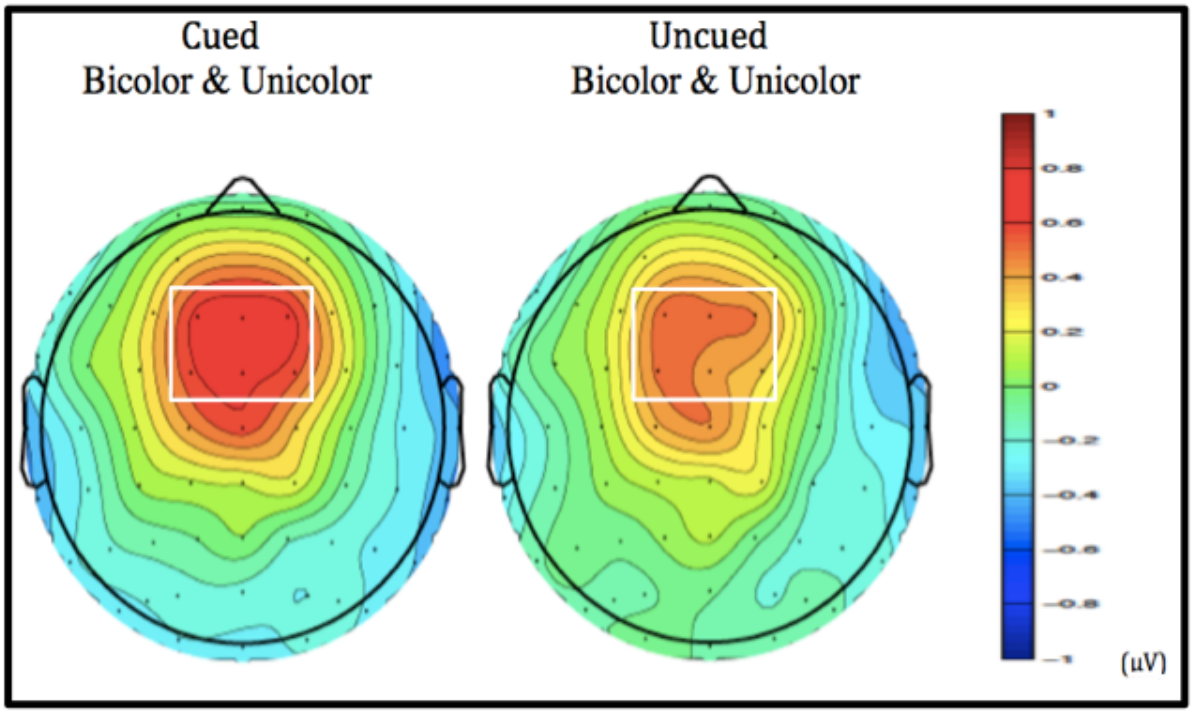

Figure 15: Main Effect of Cueing. Scalp maps for frontal electrodes (F1, FZ, F2, FC1, FCZ, & FC2) showing the voltage change for the cued bicolor & unicolor and uncued bicolor & unicolor conditions occurring at mean amplitude of 250ms to 450ms for all participants with an accuracy rate of over 50%.

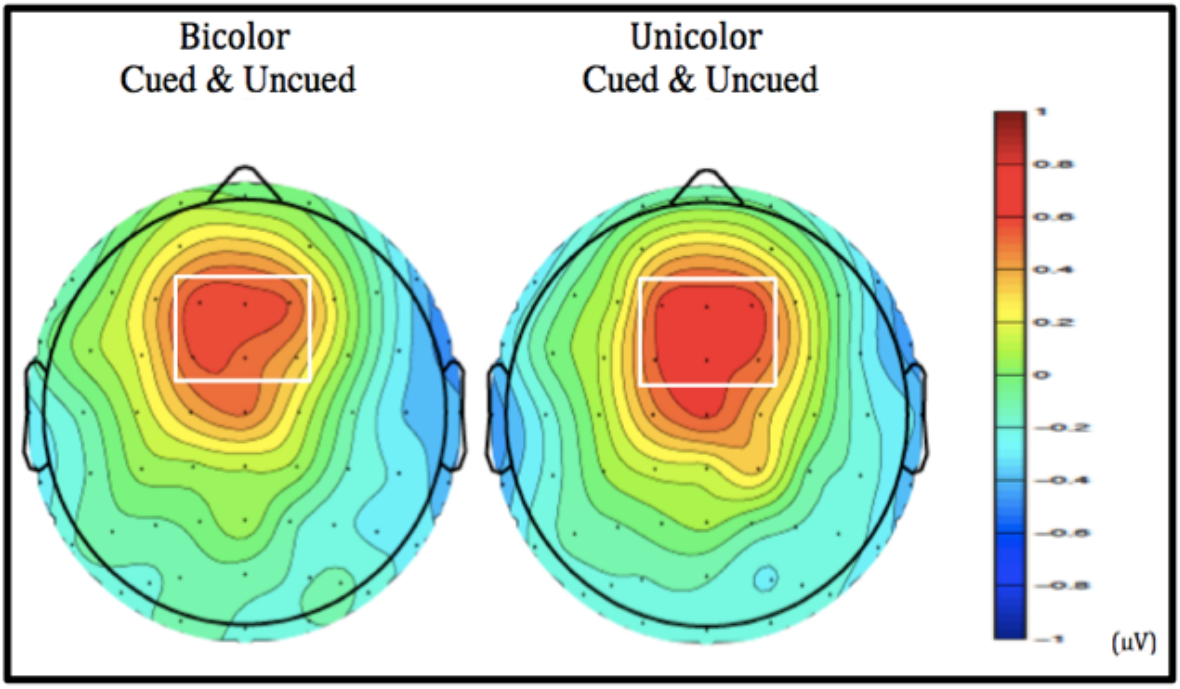

Figure 16: Main Effect of Color. Scalp maps for frontal electrodes (F1, FZ, F2, FC1, FCZ, & FC2) showing the voltage change for the cued bicolor cued & uncued and unicolor cued & uncued conditions occurring at mean amplitude of 250ms to 450ms for all participants with an accuracy rate of over 50%.

Two 2(cue) x 2(hemisphere) mixed designed ANOVAs were conducted to compare the cued and uncued conditions within each color condition. The results had the opposite effect of the other areas analyzed as they provided no evidence of a significant cueing effect within the bicolor condition ($F(1,17)=2.2$, $p=0.154$), but did show a significant cueing effect within the unicolor condition ($F(1,17)=5.1$, $p=0.038$) (see Figures 17, 18, & 19).

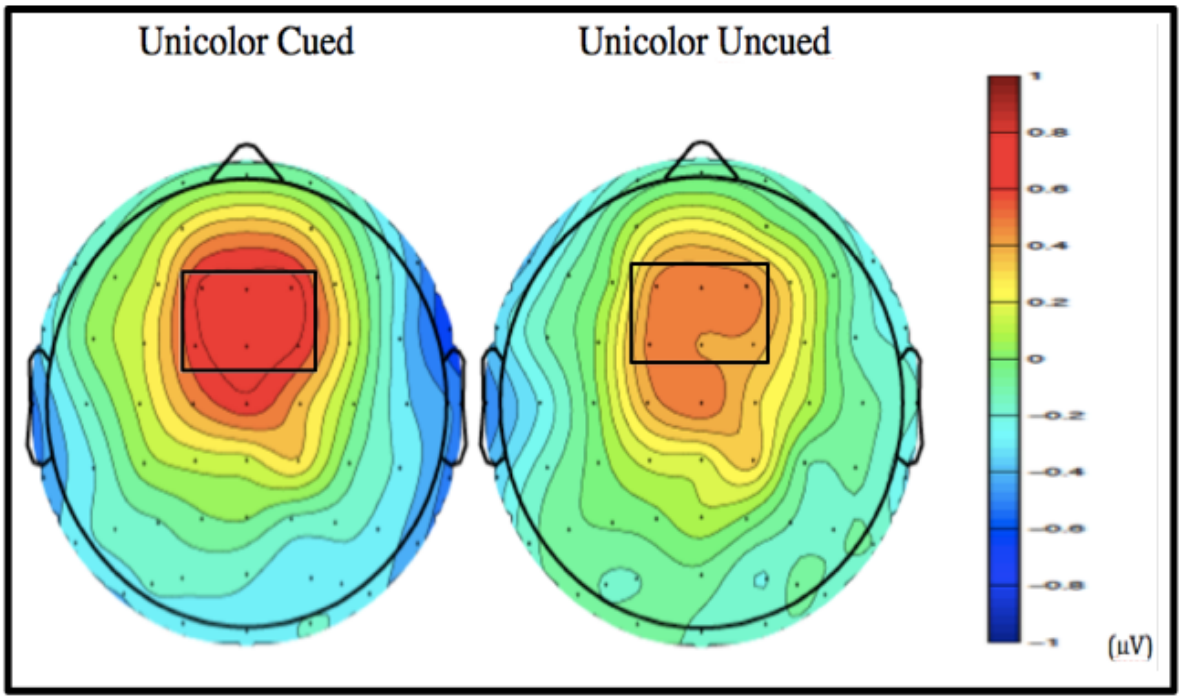

Figure 17: Cueing Effect in the Unicolor Condition. Scalp maps for frontal electrodes (F1, FZ, F2, FC1, FCZ, & FC2) showing the voltage change for the unicolor cued and unicolor uncued conditions occurring at mean amplitude of 250ms to 450ms for all participants with an accuracy rate of over 50%.

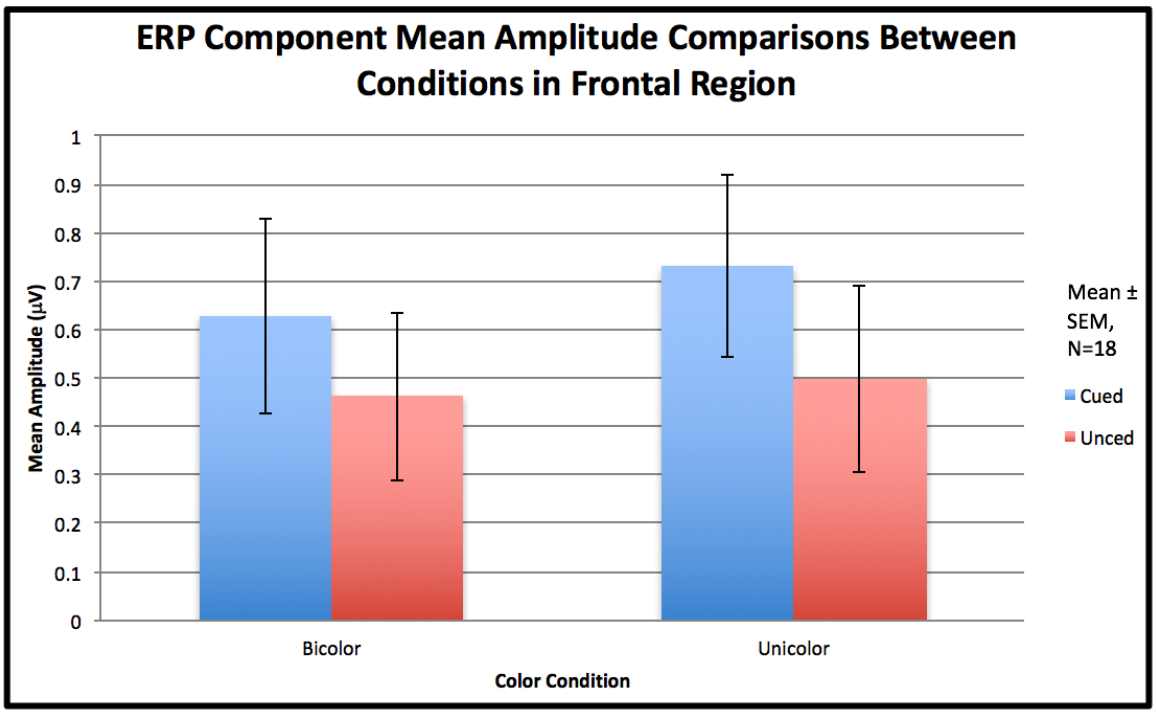

Figure 18: ERP Amplitudes across all Conditions. Bar graphs showing the mean amplitude in μV for the bicolor cued, bicolor uncued, unicolor cued, and unicolor uncued conditions in frontal electrodes (F1, FZ, F2, FC1, FCZ, & FC2) occurring at 250ms to 450ms for participants with an accuracy rate of over 50%.

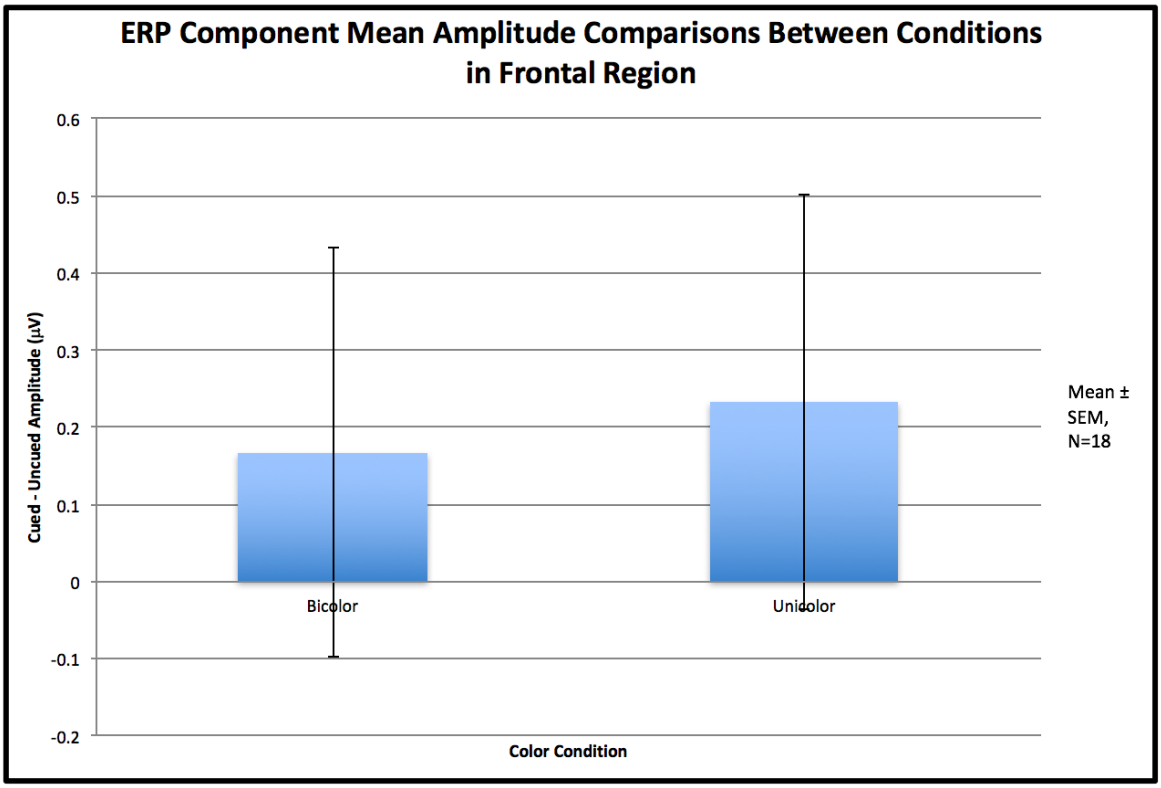

Figure 19: ERP Cueing Effect per Color. Bar graphs showing the mean amplitude difference in μV between the cued and uncued conditions for the bicolor and unicolor conditions in frontal electrodes (F1, FZ, F2, FC1, FCZ, & FC2) occurring at 250ms to 450ms for participants with an accuracy rate of over 50%.

Discussion

Cueing Effect

The behavioral results showed that direction judgments of the cued surface were more accurate than those made of the uncued surface across both the bicolored and the unicolored conditions. Correspondingly, this cueing effect was also found across both bicolored and unicolored conditions in the electrophysiological data from the parietal and the frontal electrodes. Upon further analysis, the bicolored condition was driving the cueing effect for the

parietal electrodes and the unicolored condition was driving the cueing effect for the frontal electrodes. This suggests that the advantage provided by distinguishing colors allowing for stronger object-based selection is driven by the parietal regions of the brain.

Previous research utilized an endogenous color cue to select one of two superimposed surfaces that differed in color (Valdes-Sosa et al, 1998) which resulted in a suppression of ERP components (P1 and N1) associated with unattended stimuli. A behavioral study by Reynolds et al. (2003) also showed an object-based cueing effect, this time using a delayed onset of one of two superimposed surfaces as an exogenous cue. Our exogenous cueing paradigm produced results that were also similar to that of Valdes-Sosa et al which used an endogenous cue. This suggests that neurons for the two surfaces are in competition with one another and object-based selection resulted when cueing causes one surface to win the competition temporarily.

Color Differences Enhance Object-Based Selection

A color difference between the surfaces resulted in there being a greater difference in performance between the cued and uncued conditions (with a significantly poorer performance in the uncued condition) in comparison to when the surfaces were the same color. There was not an increase in performance in the cued bicolored condition as there may be a ceiling performance for a brief translation that is only 60% coherent. This is in accordance with the theory of perceptual load which concludes that a higher task load (bicolored stimulus) allows for less capacity to attend to task-irrelevant information or in this case uncued information and therefore disallowing its inference (Lavie, 1995). We found that the addition of color segmentation between the superimposed surfaces resulted in greater suppression of the uncued surface, as measured by behavioral performance, consistent with previous research (Perry & Fallah, 2012). In that study, the addition of a color difference between the two superimposed surfaces reduced

the processing time required to determine both directions of motion. Therefore, overall the addition of color segmentation between the superimposed surfaces increases the strength of the object file, which increases the strength of object-based selection, and thus the difficulty in making judgments of a translation on an uncued surface. The cueing effect was significantly larger when the objects differed in color (bicolored) than when they were the same color (unicolored). This confirms our hypothesis that the additional distinguishing feature of color strengthens the surface selection and thus selection of superimposed surfaces in the dorsal stream is dependent on object files.

This cueing effect in the bicolor conditions versus the unicolor condition is a novel finding. When looking at the higher performers' occipital and parietal regions of the scalp, there is a significant main effect of cue in the bicolor condition that is also present when comparing the mean amplitudes of the cued and uncued ERP components P2, N2, and P3. This suggests that the areas that give rise to these components are modulating the strength of object-based selection. The visual P2 component has been shown to be generated in the parieto-occipital regions of the brain (Freunberger et al., 2007). There has also been research to show that the P2 in monkeys is originated in area V2 of extrastriate cortex (Mehta et al., 2000). The visual P2 component is involved in cognitive tasks such as selective attention (Johnson, 1989; Hackley et al., 1990; Hillyard et al., 1973), feature detection processes (Luck & Hillyard, 1994), working memory (Lefebvre et al., 2005; Wolach & Pratt, 2001), short-term memory (Golob & Starr, 2000), memory performance (Dunn et al., 1998), semantic processing (Federmeier & Kutas, 2002), priming tasks and repetition suppression (Gruber & Muller, 2004; Rossell & Nobre, 2003; Wiggs & Martin, 1998). The visual N2c component, a subcomponent of N2 that has been observed in the posterior area of the scalp, has been shown to be generated in the occipito-

temporal and occipital cortex, including area V4 (Anllo-Vento et al., 1998; Hopf et al., 2000; Hopf et al., 2006; Luck et al., 1997; Luck et al., 1997; Martinez et al., 2001). This component represents the visual attention necessary for stimuli context and feature processing in the visual cortex (Folstein & Van Petten, 2008). It has also been shown that the N2c peak may reflect category-specific processing (Allison et al., 1999), as well as response inhibition (Jodo & Kayama, 1992; Gemba & Sasaki, 1989; Sasaki & Gemba, 1993). The P3b component, a subcomponent of P3 that has been observed in the posterior area of the scalp, originates from the medial temporal lobe (Neshige & Luders, 1992; O'Donnel, ERP Peaks Review 16 et al., 1993) including the hippocampal region (Paller et al., 1992), parahippocampal gyrus, amygdala, thalamus (Katayama et al., 1985), superior temporal gyrus (Papanicolaou et al., 1992; Rogers et al., 1991), as well as the temporo-parietal junction (Knight et al, 1989; Hegerl & Frodl-Bauch, 1997). This component is involved in memory updating (Donchin & Coles, 1988), stimulus discrimination and response preparation (Verleger, 1988). Color differences strengthening object representation and object-based selection are thus reflected in modulations of these ERP components, which resulted in the behavioral differences seen.

Circuitry and Mechanism

The effects of color and cueing and their interactions were mediated by different brain regions. Color differences between the objects showed a greater difference in the mean amplitudes of the P2, N2, and P3 components over parietal electrodes, and in the mean amplitudes of the P1 and N1 components over occipital regions in the high performers. Color differences suppressed direction discrimination of the uncued surface mediated by larger ERP component differences between cued and uncued surfaces across occipital, parietal, and frontal areas of the brain in the high performers.

The P1 and N1 components arise from the dorsal extrastriate cortex and a later region of the component arises from the fusiform gyrus (Di Russo et al., 2002). The P1 and N1 components over the occipital electrodes are associated with spatial and selective attention (Di Russo et al., 2002; Pinilla et al., 2001; Khoe et al., 2005) and the N1 component has additionally been shown to be associated with discriminative processing (Hopf et al., 2002; Ritter et al., 1979; Vogel & Luck, 2000). The P1/N1 complex was reduced in amplitude when the target translation occurred on the cued surface compared to when it occurred on the uncued surface. A possible reason for this is that the occipital lobe is receiving the object-based selection feedback from the parietal lobe and thus suppressing neurons associated with the motion features of the uncued surface. When translation occurs on the uncued surface, the motion changes to directions that were not suppressed therefore resulting in an increase in uncued activity.

Although there was not a distinguishing color effect observed in the occipital region of the brain, when the bicolor cued and uncued ERP component amplitudes were compared to the unicolor cued and uncued ERP component amplitudes, the bicolor components were larger. This might be because the representation of an object recruits more neurons when there are more features present in the object. Consistent with this, there was a significant cueing effect in the bicolor condition. The difference between the mean ERP amplitudes for the P1/N1 complex of the cued and uncued condition was larger in the bicolor condition than in the unicolor condition. This suggests that there was a greater suppression of the uncued surface due to the object-based selection feedback from the parietal lobe.

In the parietal and frontal region of the brain, the components that were analyzed were the P2, N2, and P3 components. The P2 component is associated with target stimulus features. The N2 component is associated with spatial deviance, as well as focal attention on the target

and possible suppression of non-target stimuli (Eimer, 1996). It is also associated with target probability and task difficulty (Duncan-Johnson & Donchin, 1977; Israel et al., 1980). In both the parietal lobe and the frontal lobe, the amplitudes of the P2/N2/P3 complex components were greater for the cued trials than the uncued trials in both color conditions. Thus, the cueing effect found in the parietal and frontal ERP components was due to object-based selection, since the objects were superimposed.

When comparing the difference in amplitudes between the cued and uncued conditions within each color condition, different effects were found in the parietal and frontal lobe. In the frontal lobe, the cueing effect on the amplitudes of the P2/N2/P3 complex components was greater for the unicolor condition in comparison to the bicolor condition. The greater amplitude difference in the unicolor condition may have been due to increased executive function due to greater task difficulty as two surfaces of the same color are more difficult to differentiate from one another. In the parietal lobe, the cueing effect was stronger in the bicolor condition. The target cued surface had stronger object-based selection when the two surfaces were different colors and thus participants were better able to attend to the cued surface and suppress the differently colored uncued surface making it more difficult to determine the translation direction of the uncued surface in the bicolored condition behaviorally. Using color differences to distinguish the objects further thus increases the strength of the object file which results in enhanced cueing effects on the ERP components in the parietal region of the brain. Thus, the parietal components were consistent with the behavioral results: object-based selection and the related parietal components were stronger when the surfaces were differentiated by color.

Conclusion

This study sought to shed light on feature integration and object-based selection through the use of superimposed surfaces with different degrees of distinguishability. Through a combination of paradigms from prior studies, we developed a modified exogenous cueing paradigm to compare the behavioral and event related potential comparisons of direction discriminability while varying how distinguishable the two objects were. We found that the addition of a color difference allowed for greater object-based selection and suppressed performance in discriminating the direction of motion of the uncued surface over the cued surface. This was driven by greater suppression of the uncued surface. These behavioral results were also reflected in the ERP components. The difference between the mean ERP amplitudes for the P2/N2/P3 components in the parietal region was larger in the bicolor condition than in the unicolor condition thus representing a featural distinguishability effect on object based selection. The reverse effect was found in the frontal region with the difference between the mean ERP amplitudes for the P2/N2/P3 components being larger in the unicolor condition, likely due to the increased difficulty in distinguishing the two objects. These novel findings support our theory that color and motion integrate to form an object file within the dorsal stream and that the strength of object-based selection in the dorsal stream depends on how distinguishable the objects are. Therefore, when an object is selected, there is suppression of distractors where the suppression is based on features not shared with the selected object. In fact, it may be that the more features that can distinguish the distractor from the selected object, the more ways its object file can be suppressed.

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Chapter 4: General Discussion

Applications

This study not only helps to solve the binding problem but it also has several important applications. Data visualization, display design, user interfaces amongst other applications can be designed to use color differences in concert with cueing by flashes, flickering, and brightening to suppress attention grabbing power of surrounding stimuli. This mechanism can be used to help pilots with complex cockpit displays as well as data visualization of traffic flow in smart cities and other Big Data projects. As for clinical applications, schizophrenic populations have problems with feature integration that may be causing some of the disturbances in their consciousness (Bob, 2007). These results add to the growing body of knowledge on how binding works, which should eventually lead to helping these individuals with feature integration.

Caveats

There are several caveats and concerns to consider in this study that may require further investigation. The first is that we did not perform source localizations as we only had 64 channels. Source localizations are more accurate with a minimum of 128 electrodes. However, the ERP components we analyzed are common in the literature, and have been source localized in many prior studies. It is with these known sources in mind that conclusions about the underlying circuitry were made. From those prior source localizations, the results of this study show that the dorsal extrastriate cortex and the fusiform gyrus are involved in exogenous cueing. The parieto-occipital, the deep parietal regions, the frontal regions, the insula, and the inferior temporal areas of the brain are involved in object-based selection as they show a cue by color interaction.

Another caveat is that we focused our analyses on the high performers. We removed the low performers on the assumption that their performance was based on weaker object-based selection. By focusing on high performers, we biased our results towards finding areas involved in object-based selection. However, this does suggest that object-based selection varies across the population. Similar inter-individual differences have been found in spatial attention paradigms (Huttermann & Memmert, 2014). This means that while color differences can be used to increase suppression of distractions when using displays, the amount of suppression will vary by individual.

Future Directions

While the current study shows that the suppression that arises from object-based selection is strengthened when an irrelevant feature better distinguishes them, we do not yet know whether this selection can be increased by adding additional distinguishing features. The first stage would be to test distinguishing features other than color such as using shape or form in place of color. Then several distinguishing features could be using together to determine if the suppression is additive. This would be apparent in the behavioral results, as participants would perform even worse when determining the direction of the translation of the uncued surface when it is separated but a different rotation direction, color, and shape. The ERP component would also be further suppressed for the uncued surface that has the most features integrated into its object representation.

A further suggestion would be to add additional objects into the competition. With three objects present in the stimuli, would the suppression of the 2 uncued objects be of equal strength to when there was a single uncued object, or would the suppression be split between them? If the suppression of each of the two uncued objects is the same as when there was one uncued object,

the ERP component would be expected to have a similar amplitude as the current study. However, if the suppression of the uncued objects are to be divided, the ERP components for these objects would not be as suppressed as in the current study.

As well, a study can be conducted placing the two surfaces in different eye fields to determine early versus late object selection. As eye effects occur in V1 and after V1 there is no eye of origin information, if the strength of the suppression behaviorally and in the EEG data varies when the stimuli is presented in each eye monocularly versus in both eyes, this is an indication that the effects are occurring as early as V1. Thus, this type of experiment would help to determine the earliest stage of increased suppression based on object distinguishability matters.

Chapter 5: General Conclusion

The more features distinguish two objects, when one object is cued, the greater the suppression of the other object. This novel finding supports the theory that the features of color and motion are integrating to form an object file with increased representation in the brain than that of an individual feature. Although source localization was not performed in this study, we have discussed the different effects in the different areas of the brain in accordance with the ERP components. This new information adds to the knowledge of feature integration and object-based selection, as well as towards a comprehensive model of object representations within the dorsal stream. The results can be applied to enhancing the effectiveness of items of interest in data visualization settings, as well as used clinically with patient populations having difficulty integrating features.

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